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FRUIT-BUD DEVELOPMENT IN STRAWBERRY VARIETIES AND SPECIES[1]

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INTRODUCTION

Investigations in fruit-bud formation in the strawberry have hitherto been confined to a few well-known varieties. The results obtained from such investigations have greatly aided both the breeder of strawberries and the investigator studying cultural practices. However, in order better to understand the relationship of fruit-bud formation to cultural practices when applied to different varieties, it has been found necessary to determine how fruit-bud initiation occurs and development proceeds in a wide range of variety types and species.

This report is the result of a study of the course of fruit-bud development in representative varieties and in several species, made at the United States Plant Field Station, Glenndale, Md., about 15 miles from Washington, D. C.

HISTORY

The time of fruit-bud formation in the strawberry was first studied in Wisconsin by Goff,[2] who found that in 1899 in the Clyde variety it occurred in late September. Morrow [3] in Iowa in 1906 found traces of fruit-bud differentiation in the Dunlap and Warfield varieties by September 18. Studies by Hill and Davis [4] at Ottawa, Canada, indicate that fruit-bud differentiation occurs about September 19. Ruef and Richey [5] in Iowa found fruit-bud formation in the Dunlap taking place by September 7. Darrow [6] concluded that in certain parts of California fruit-bud formation must occur throughout the summer and probably during the winter months, as the fruit continues to mature throughout the year. From a survey made in 1923 of several varieties of strawberries at different experiment stations from Massachusetts to Minnesota, Darrow [7] concluded that fruit-bud differentiation takes place during the latter part of September, occurring slightly in advance in the early varieties. He stated that in all sections fruit buds were visible to the unaided eye by the middle of October.

[1] Received for publication June 12, 1929; issued March, 1930.

[2] GOFF, E. S. INVESTIGATIONS OF FLOWER BUDS. Wis. Agr. Expt. Sta. Ann. Rpt. 17: 266-285, illus. 1900.

[3] MORROW, H. E. A STUDY OF THE FORMATION OF FLOWER BUDS WITH SPECIAL REFERENCE TO THE STRAWBERRY. 1907. [Unpublished thesis. Iowa State Col. Agr. and Mechanic Arts, Ames.]

[4] HILL, H., and DAVIS, M. B. STUDIES IN STRAWBERRY BUD DIFFERENTIATION. Canada Dept. Agr. Bul. (n. s.) 110, 15 p., illus. 1929.

[5] RUEF, J. U., and RICHEY, H. W. A STUDY OF FLOWER BUD FORMATION IN THE DUNLAP STRAWBERRY. Amer. Soc. Hort. Sci. Proc. 22: 252-260. 1925.

[6] DARROW, G. M. ESSENTIALS IN STRAWBERRY CULTURE. PART III. FRUIT BUD FORMATION. Amer. Fruit Grower Mag. 46 (6): 7, 18-19, illus. 1926.

[7] See footnote 6.

MATERIALS AND METHODS

The studies herein reported were conducted during the late summer and autumn months of 1926, 1927, and 1928. The investigations made in 1926 and 1927 were more or less preliminary to the more complete studies made in 1928. Only representative varieties and species of the various types of strawberries were selected. Early varieties such as the Campbell and Excelsior, late varieties such as the Chesapeake, varieties grown in the South such as Klondike and Missionary, northern varieties such as Dunlap and Portia, and Ananas de Guemene, a European variety, were studied.

Selection No. 27 from Highlands, N. C., was chosen as representative of *Fragaria virginiana* Duchesne, the wild strawberry of the eastern part of the United States. This selection is late in maturing, and it is possible that earlier forms of this species might have been found. *F. chiloensis* (L.) Duchesne, which is native to the Pacific coast, is probably always late in maturing. The plants used were the progeny of plants from the beaches of Oregon. The one form of *F. nilgerrensis* Schlechtend, a species native to northern India, which was available, was late. *F. americana* (Porter) Britton is an American representative of *F. vesca* L., the wood strawberry of Europe, and matures its fruit late.

The varieties of strawberries studied in 1927 and 1928, which include most of those previously reported by other investigators, are listed below. Howard 17 was the only variety studied in 1926.

1927	
Ananas de Guemene.	U. S. D. A. No. 25.
Black Hautbois (*Fragaria moschata*).	U. S. D. A. No. 854.
Belt.	Vantage.
Campbell.	White sugar.
Chesapeake.	
Dunlap.	1928
Erige du Poitou (*F. vesca*).	
Ettersburg 80.	Ananas de Guemene.
Ettersburg 121.	Aroma.
Excelsior.	Campbell.
F. americana.	Chesapeake.
F. chiloensis.	Dunlap.
F. nilgerrensis.	Erige du Poitou (*F. vesca*).
F. virginiana No. 27.	Excelsior.
Heflin.	*F. americana.*
Howard 17.	*F. chiloensis.*
Joe.	*F. nilgerrensis.*
John Ruskin.	*F. virginiana* No. 27.
Kalicene.	Heflin.
Little Scarlet (*F. virginiana*).	Howard 17.
Lupton.	Kalicene.
Missionary.	Klondike.
Monstrueuse Hautbois (*F. moschata*).	Missionary.
Portia.	Monstrueuse Hautbois (*F. moschata*).
Sample.	Portia.
	Sample.
	U. S. D. A. No. 25.

In 1927 material was collected every 15 days, beginning September 1 and ending October 15. In 1928 collections were made almost continuously from late August until early in November.

Studies in 1926 and 1927 followed the usual method of killing, fixing and embedding in paraffin, sectioning, and staining. Both Haidenhain's iron-alum and Delafield's haematoxylins were used, and good results were obtained by both stains. However, it was very

evident that the above methods were not adapted to the study of large numbers of buds. The results of the work in 1927 indicated that fruit-bud development, at least in the strawberry, is too variable to permit definite conclusions as to the time and rate of development to be drawn from an examination of a limited quantity of material.

During the season of 1927 runner plants of nearly the same age which had taken root early in August were used for these studies. The results obtained in 1927, however, were somewhat variable. It was considered that the variability might have been due in part to slight differences in age and in part to growing conditions not favorable to root formation by young plants. Therefore, in order to obtain more uniformity, a special planting was made in April, 1928, on a clay loam soil as uniform as it was possible to obtain, and only the mother plants from this plot were used for the studies herein reported.

It was found that, with the use of a very sharp razor, free-hand sections of as many crowns or growing points as were necessary could be cut in a short time and thin enough to give a clear idea of the range and stage of development at any particular time. As soon as cut, these sections were put in 95 per cent alcohol for 10 to 15 minutes, after which they were passed through 50 per cent alcohol, washed in water, and stained in Delafield's haematoxylin for 3 to 5 minutes. After staining, the sections were washed in water and passed through a series of gradually ascending strengths of alcohol to absolute alcohol, where they were allowed to remain about 5 minutes, then removed to xylol, and finally mounted in Canada balsam on slides.

When development had reached a stage where it was no longer necessary to use a microscope to see the fruit buds, several crowns of each variety were cut lengthwise, and the most representative were selected for photographing. It was found that if the cut tissue was allowed to oxidize until it had become a light brown the structures showed best. Photographs three times the actual size were then obtained. Camera-lucida drawings of the mounted sections were made for comparison. It was possible to classify the early stages by the use of the drawings and the later stages by the photographs.

PROCESS OF FRUIT-BUD FORMATION

Goff [8] regarded the broadening of the crown or growing point accompanied by the assumption of an irregular outline as an indication of an early stage of flower development in the strawberry. For these studies definite fruit-bud differentiation was considered to have taken place in the strawberry when the growing point had become broad and somewhat flattened on top. At this stage elongation begins immediately, and when the flower stalk starts to lengthen new growing points appear at the base, which develop into secondary flowers or other flower stalks. Further elongation results in tertiary and quaternary flowers differentiating on the flower stalk just behind the secondary and primary flowers.

Ruef and Richey [9] state that the degree of development of the flower parts varies according to the respective flower buds on the fruit stalk. They also give the order of development as sepals, petals, stamens,

[8] See footnote 2. [9] See footnote 5.

and pistils. Their findings are corroborated in the present study, for soon after the elongation of the flower stalk begins the rudiments of the sepals appear, followed quickly by the petals and stamens. Some time elapses after rudimentary sepals, petals, and stamens have differentiated before the pistils appear on the receptacle. Pistil development begins on the edges of the receptacle and advances toward the center. It is following the appearance of these pistils on the primary flower that rapid elongation of the flower stalk begins.

INDICATIONS OF FRUIT-BUD FORMATION

It was found that the broadening of the growing point, which is considered the first definite indication of fruit-bud differentiation, is preceded (1) by the thickening of the crown, so that the last differentiated rudimentary leaves appear almost on the same level as the vegetative growing point, and (2) by the growing point itself beginning to be dome shaped. These indications were most noticeable in Howard 17, Campbell, and Kalicene in the latter part of August. Perhaps the crowns of other varieties and species thicken in some degree during the fall months under Maryland conditions.

Such indications as have been described occurred over a period of a few days in some varieties to as much as one month in others before definite fruit-bud differentiation could be seen. Some idea of the conditions found during the 1928 season may be obtained from Table 1. The periods given in the table are not assumed to be indicative of the development of all buds, for during the same period many crowns were found with typical vegetative growing points.

TABLE 1.—*Period covered by indications of fruit-bud differentiation and the approximate date of definite fruit-bud formation in 14 varieties and 4 species of strawberries in 1928*

Variety or species	Period covered by indications of fruit-bud differentiation	Date of definite differentiation in the majority of the crowns	Variety or species	Period covered by indications of fruit-bud differentiation	Date of definite differentiation in the majority of the crowns
Ananas de Guemene	Sept. 24–Oct. 5	Oct. 6	Fr. virginiana No. 27		Oct. 4
Aroma	Sept. 6–Oct. 3	Oct. 3	Heflin	Aug. 28–Oct. 1	Oct. 1
Campbell	Aug. 25–Sept. 15	Sept. 18	Howard 17	Aug. 25–Sept. 14	Sept. 14
Chesapeake	Sept. 7–Oct. 4	Oct. 4	Kalicene	Sept. 6–Sept. 27	Sept. 25
Dunlap	Aug. 30–Sept. 27	Sept. 27	Klondike	Sept. 7–Sept. 26	Oct. 3
Excelsior		Sept. 28	Missionary	Sept. 18–Sept. 27	Sept. 27
Fragaria americana	Sept. 19–Oct. 5	Oct. 5	U. S. D. A. No. 25	Aug. 27–Sept. 22	Sept. 20
F. chiloensis		Oct. 6	Portia	Aug. 28–Sept. 27	Sept. 27
F. nilgerrensis	Oct. 10–Nov. 20	Nov. 20	Sample	Sept. 18–Sept. 27	Sept. 23

It can not be concluded that all growing points take 15 to 30 days to pass from the stage of the first noticeable broadening of the growing point until definite elongation of the flower stalk is noticeable. Doubtless some of the early broadening crowns actually differentiated before the date set when definite differentiation was most general. Figure 1 shows the growing point of the Kalicene variety already beginning to elongate on September 1, 1927. Howard 17 and

Campbell also showed the beginning of definite fruit-bud formation on this date. It is believed that some unusual conditions existed in 1927 which caused a few crowns to differentiate fruit buds earlier than is usual for these varieties. In 1928 Howard 17 and Campbell showed indications of fruit-bud differentiation by September 1 and Kalicene by September 6, but no definite fruit-bud development was found in the above three varieties until September 14, or later.

FIGURE 1.—First evidence of definite fruit-bud differentiation in the Kalicene strawberry: Growing point (A) just beginning to elongate, September 1, 1927. × 80

DEFINITE FRUIT-BUD FORMATION

There is little doubt that fruit-bud differentiation has already taken place when the growing point becomes as broad and flattened on the top as Figure 1 shows. At this stage elongation begins immediately. Table 1 gives the approximate dates of definite fruit-bud differentiation in most of the 1-year-old mother plants of each variety studied in 1928. Table 2 gives the dates when definite differentiation was found in 1927.

Definite fruit-bud formation was found during the latter half of September and early in October in all varieties and species studied with but one exception. These results are in close agreement with those of Darrow,[10] who concluded that fruit-bud differentiation took place during the latter part of September in sections of the northern United States.

TABLE 2.—*Approximate dates when definite fruit-bud formation was found in most of the crowns of 10 varieties of strawberries in 1927*

Variety	Definite differentiation indicated by elongation of growing point	Secondary and tertiary flower stalks appearing	Variety	Definite differentiation indicated by elongation of growing point	Secondary and tertiary flower stalks appearing
Campbell	Sept. 1	Oct. 1	John Ruskin	Oct. 1	Oct. 15
Ettersburg 80	Oct. 15	Nov. 3	Kalicene	Sept. 1	Oct. 1
Ettersburg 121	do		Missionary	Oct. 1	Oct. 17
Heflin	Sept. 15		U. S. D. A. No 25	Sept. 15	Oct. 1
Howard 17	Sept. 1	Sept. 15	Sample	Oct. 1	Oct. 17

Fruit-bud differentiation was found to cover a considerable period in some varieties, Kalicene being notable in this respect. In this variety differentiation was spread over a period of one month, crowns

[10] DARROW, G. M. [Letters reporting to the cooperating experiment stations.] 1923.

of some plants showing the first stages one month earlier than others. *Fragaria chiloensis* was also found to be somewhat variable, but in general the varieties differentiating first were more variable than those differentiating later.

The species were all found to be late in differentiating (Table 3), particularly *Fragaria nilgerrensis*, native to northern India. This species did not show any definite differentiation until November 27, when development indicated that probably it took place about November 20. Although fruit-bud differentiation in different plants of all the varieties studied was spread over a period of about three weeks, it is possible to classify them roughly according to the time when the initiation process is most general. Such a classification is shown in Table 4. The more limited studies in 1926 and 1927 seem to verify this grouping.

TABLE 3.—*Classification of varieties and species of strawberries according to the time of the initiation of the process of fruit-bud formation in 1928* [a]

Early	Midseason	Late	Very late
Campbell. Howard 17. Kalicene. Sample. U. S. D. A. No. 25.	Dunlap. Excelsior. Heflin. Missionary. Portia.	Aroma. Ananas de Guemene. Chesapeake. Klondike. Fragaria chiloensis. F. americana. F. virginiana No. 27.	Fragaria nilgerrensis.

[a] Additional studies made in the fall of 1929 on these varieties indicate that this classification is the same for 1929, except for Excelsior, which was in the early class, and Sample, which was in the midseason or late class. Studies in 1929 indicate the following classification of other varieties:

Early	Midseason	Late
U. S. D. A. No. 652. U. S. D. A. No. 655. U. S. D. A. No. 542. U. S. D. A. No. 668. Gene.	Blakemore. Oregon. U. S. D. A. No. 672. U. S. D. A. No. 632.	Bedarena. Sybil. F. vesca type from Grangeville, Idaho. Pearl. Judith. Joe. Ettersburg 121. U. S. D. A. No. 845 U. S. D. A. No. 44.

DEVELOPMENT OF THE FRUIT BUD

It is during the development of fruit buds that the most significant differences between varieties appear. In order to show this trend, a classification is given of the different stages in the process that take place during the autumn. Table 4 gives the dates at which the different varieties and species reached the various stages. Figure 2 shows graphically the process of development in a few representative varieties and species as illustrated in Figures 3 to 9.

Table 5 gives the interval in days between the different stages in the process of development for the varieties and species studied. This classification was based entirely upon the development of the primary flower. It was found from a limited study that the development in the primary, secondary, and tertiary flowers in general is proportional, and is in agreement with the results of Ruef and Richey [11] with the Dunlap strawberry.

[11] See footnote 5.

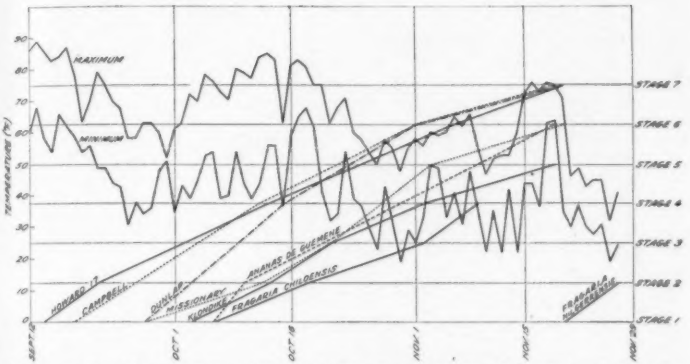

FIGURE 2.—Graphic presentation of the trend of development in the fall of 1928 in certain strawberry varieties representative of those studied

FIGURE 3.—Definite fruit-bud differentiation of the Sample strawberry, representing stage 1 in Figure 2, October 1, 1927. × 80

FIGURE 4.—Rudiments of first, secondary, and tertiary flowers appearing on the Sample strawberry, representing stage 2 in Figure 2, September 26, 1928. × 80

FIGURE 5.—Rudimentary flower parts, except pistils, on the Missionary strawberry, representing stage 3 in Figure 2, October 15, 1927. × 80

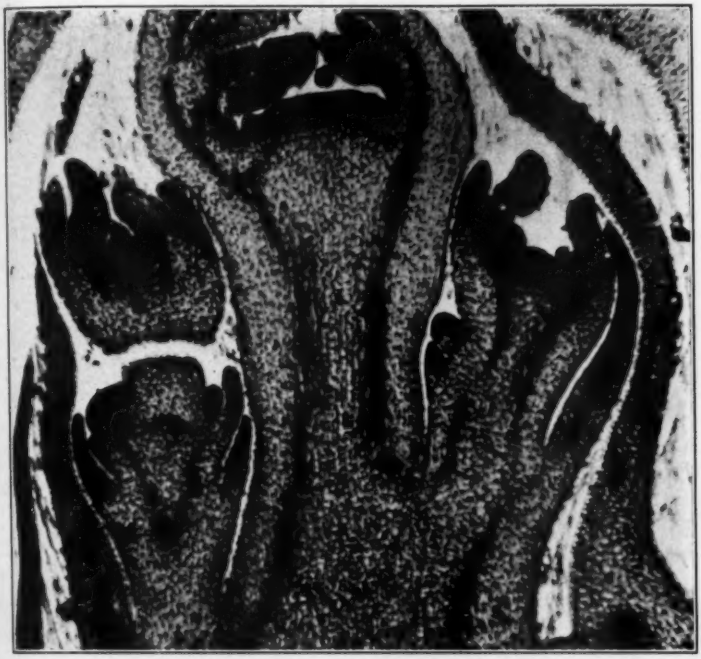

FIGURE 6.—First rudimentary pistils appearing on the primary flower of the Campbell strawberry, representing stage 4 in Figure 2, October 1, 1927. × 80

FIGURE 7.—Rapid elongation of the primary flower stalk of the Howard 17 strawberry just beginning, representing stage 5 in Figure 2, November 1, 1928. × 3½

FIGURE 8.—Elongated flower stalk of the Missionary strawberry, buds formed but not ready to open, representing stage 6 in Figure 2, November 20, 1928. × 3¾

FIGURE 9.—Primary flowers of the Excelsior strawberry ready to open, representing stage 7 in Figure 2, November 20, 1928. × 3¾

TABLE 4.—*Approximate dates upon which the 14 varieties and 4 species of strawberries were found to be in the various stages of development in 1928*

Variety or species	Primary, secondary, and tertiary flowers appearing	Rudimentary flower parts present, except pistils	First pistils appearing on primary flowers	Rapid elongation of primary flower stalk begun	Buds formed but not open	Primary flower buds ready to open or already in bloom
Aroma	Oct. 10	Oct. 18		Nov. 5	Nov. 20	
Ananas de Guemene	do	Oct. 20	Nov. 2	Nov. 9	Nov. 19	
Campbell			Oct. 12		Nov. 1	Nov. 19
Chesapeake	Oct. 10	Oct. 20		Nov. 20		
Dunlap			Oct. 15		Nov. 1	Nov. 19
Excelsior	Oct. 4	Oct. 20				Nov. 15
Fragaria americana	Oct. 10	Oct. 22	Nov. 2		Nov. 19	
F. chiloensis	Oct. 18	Nov. 2	Nov. 9			
F. nilgerrensis	Nov. 27					
F. virginiana	Oct. 12	Oct. 20		Nov. 19		
Heflin	Oct. 10	Oct. 15		Nov. 1	Nov. 19	
Howard 17	Sept. 21		Oct. 13	do	Nov. 6	Nov. 20
Kalicene	Sept. 30	Oct. 13			Nov. 1	Do.
Klondike	Oct. 13	Oct. 20	Nov. 2	Nov. 19		
Missionary	Oct. 12	do		Nov. 1	Nov. 20	
U. S. D. A. No. 25	Sept. 25	Oct. 10	Oct. 15		Nov. 1	Nov. 20
Portia	Oct. 13			Nov. 6	Nov. 18	
Sample		Oct. 20			Nov. 20	

In general, the degree of development reached at the end of the growing season of 1928 was in more or less correlation with the time of fruit-bud differentiation. But from Figure 2 it appears that under the conditions of these experiments different varieties follow different courses of development. Missionary and Dunlap, for example, begin fruit-bud differentiation about the same time. Development immediately following differentiation in Missionary is somewhat slow compared with that in Dunlap; later, its development becomes very rapid for a time and finally slows up. In contrast, the fruit bud of the Dunlap makes a rapid development at first which gradually becomes relatively slower toward the end of the season. Howard 17, although beginning early, never at any time develops very rapidly. However, because of its early start, it is one of the most fully developed varieties throughout the season.

TABLE 5.—*Approximate number of days from date of definite fruit-bud differentiation of strawberies to the various later stages of development in 1928*

Variety or species	Primary, secondary, and tertiary flowers appearing	Rudimentary flower parts present, except pistils	First pistils appearing on primary flowers	Rapid elongation of primary flower stalk begun	Buds formed but not open	Primary flower buds ready to open or already in bloom
Aroma	7	15	25	33	47	
Ananas de Guemene	4	14	26	33	43	
Campbell	8	16	24	34	44	62
Chesapeake	6	16	32	47		
Dunlap	6	12	18	26	35	54
Excelsior	6	22	29	35	41	48
Fragaria americana	5	17	28	36	45	
F. chiloensis	12	27	34			
F. nilgerrensis	7					
F. virginiana	8	16	31	46		
Heflin	9	14	22	30	48	
Howard 17	7	18	29	48	53	67
Kalicene	5	18	24	31	37	56
Klondike	10	17	30	47		
Missionary	15	23	29	35	55	
U. S. D. A. No. 25	5	20	25	33	42	56
Portia	16	24	32	40	52	
Sample	14	27	38	48	58	

Of even more significance than the irregularity in the rate of development is the interval of time between the different stages, which for all varieties studied averages about 10 days between successive stages. Some varieties develop consistently faster than this, others slower. Table 6 groups the varieties according to their rate of development. By comparing Table 4 with Table 6, it will be noted that certain varieties differentiate their fruit buds early and continue to make rapid growth throughout the season; such varieties are Campbell, Kalicene, and U. S. D. A. No. 25 (a cross of Van Fleet 3 × Campbell, originated at the United States Plant Field Station, Glenndale, Md.).

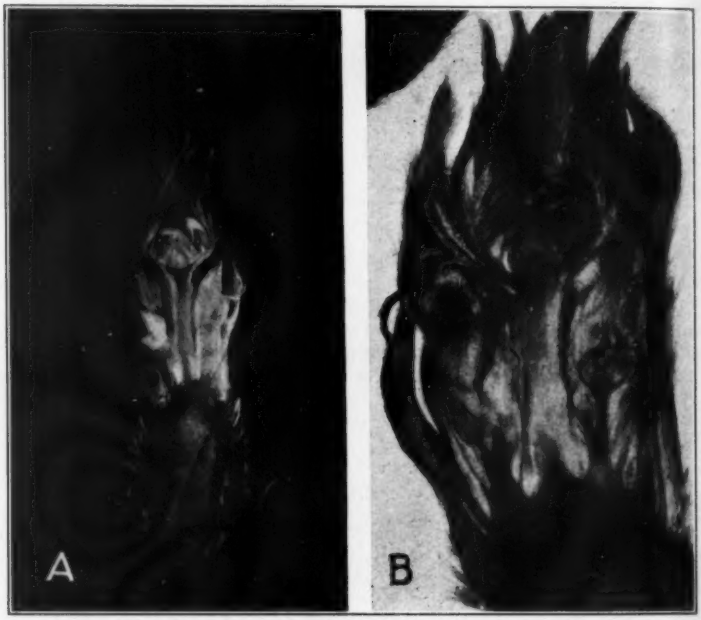

FIGURE 10.—Primary flower buds of the Dunlap strawberry just beginning to open: A, November 8, 1927; × 1¼. B, November 20, 1928; × 3¾

Howard 17 makes a slow growth and Sample a much slower growth. Dunlap and Excelsior, although differentiating fruit buds later than the sorts above mentioned, develop rapidly and at the end of the season attain the same degree of growth as Campbell.

Ananas de Guemene and *Fragaria americana*, although among the latest to differentiate fruit buds, develop very rapidly in the late fall. By November 8, 1927, there was an occasional open bloom on *F. americana*. Chesapeake, Klondike, and *F. virginiana* differentiate fruit buds late and make a more or less slow growth thereafter.

Figures 10 to 12 show a very striking similarity between the seasons of 1927 and 1928 in the degree of development in the same varieties. The primary flower occasionally comes into blossom in late fall. Secondary flowers almost never blossom, unless, perhaps, when weather conditions are very abnormal.

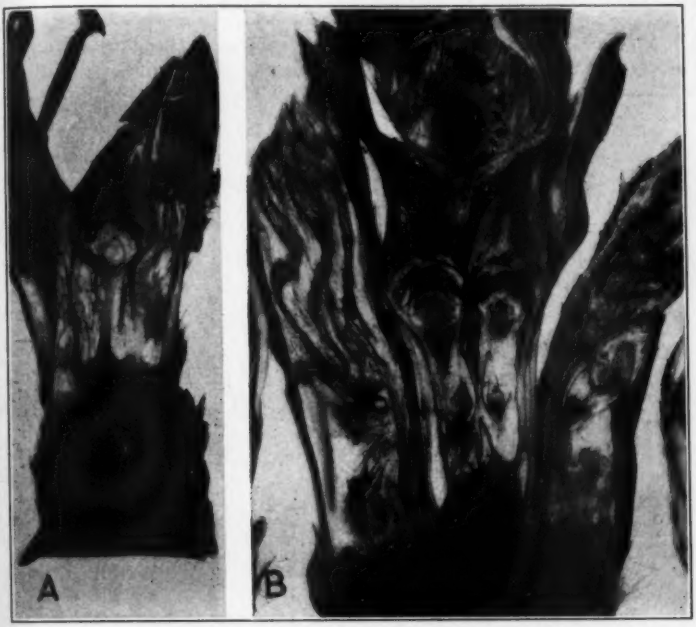

FIGURE 11.—Flower buds of the U. S. D. A. No. 25 strawberry in various stages of development: A, November 15, 1927; × 1¾. B, November 20, 1928; ×3¼

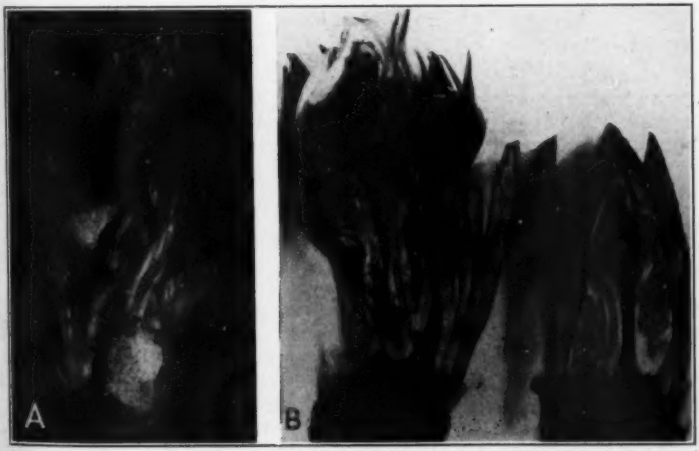

FIGURE 12.—Opening blossoms of Campbell strawberry: A, November 8, 1927. B, November 19 1928; ×1¾

TABLE 6.—*Classification of varieties and species of strawberries according to the rate of development of their fruit buds in autumn, season of 1928*

Rapid	Intermediate	Slow
Ananas de Guemene. Campbell. Dunlap. Excelsior. Fragaria americana. Kallcene. U. S. D. A. No. 25.	Aroma. Heflin. Howard 17. Missionary. Portia.	Chesapeake. Klondike. Sample. Fragaria chiloensis. F. virginiana.

In late November, 1928, open blossoms were found on some plants of many varieties, particularly Campbell, Dunlap, Excelsior, U. S. D. A. No. 25, and Howard 17. Somewhat similar conditions were found in November, 1927. As these flowers are almost always primary ones that are killed during the late fall, the secondary flowers on these plants may not open in the following spring before the primary flowers of some other variety not so well advanced at the end of the fall growing season.

Significant differences between varieties are even more striking when the ripening season is considered. In Table 7 the varieties and species are classified according to their ripening season. It will be noted that Campbell and U. S. D. A. No. 25, which were among the first to differentiate, are also among the first to ripen. Howard 17, the first variety of all to begin differentiation, is one of the first to ripen, but it does not develop as rapidly in the autumn as some other varieties, and although early blooming it is not among the very first to bloom in the spring. Dunlap, which differentiates fruit buds much later than Howard 17 but which develops rapidly and blooms early in the spring, does not ripen as early as Howard 17 under Maryland conditions, although it is early in the North-Central States, where it originated.

TABLE 7.—*Classification of varieties and species of strawberries according to their ripening season*

Early	Midseason	Late	Very late
Campbell. Excelsior. Heflin. Howard 17. Klondike. Missionary. U. S. D. A. No. 25.	Ananas de Guemene. Dunlap.	Aroma. Chesapeake. Fragaria americana. F. virginiana. Portia. Sample.	F. chiloensis. F. nilgerrensis.

Fragaria americana, although it differentiated fruit buds late, made a rapid growth in the late autumn, but failed to make a rapid growth in the spring. Chesapeake and *F. chiloensis* develop slowly during the autumn, bloom late in the spring, and ripen their fruit late in the season. Heflin, which differentiates fruit buds about midseason and makes only a moderate growth in the autumn, is among the first to bloom and to ripen in the spring. Klondike follows much the same trend in development as the Chesapeake during the autumn, but its growth is faster in the spring, and it ripens before the Chesapeake.

DISCUSSION

The results of these studies seem to indicate that the course of development of fruit buds in the strawberry family as a whole can not be definitely outlined. Each variety has a time and rate of development peculiar to itself. Although no study was made of the effect of cultural conditions upon the different varieties, it is believed that each would respond in a characteristic manner to changes in the environment. These varying responses are probably due to genetic differences that undoubtedly play a large part in the similar and dissimilar rates of development in the different varieties.

Owing to the varied parentage of the standard varieties, variations in development between different varieties under the same conditions are to be expected. With the utilization in breeding of plants obtained from remote sources, an even greater variation in response to the same set of conditions may be expected.

Fragaria nilgerrensis, native to northern India, differentiates fruit buds late in the fall. It may be expected that crossing our common varieties with such a species would enormously increase the possibilities of obtaining new varieties whose responses to environmental conditions would cover a far wider range of possibilities than that of our present varieties.

The time of fruit-bud differentiation in 1-year-old mother plants was found to be somewhat variable, particularly in Kalicene and other varieties differentiating rather early. This variability of fruit-bud differentiation in a single variety may be due to cultural practices and fertility of the soil. However, the influence of culture and of fertilizer applications on fruit-bud development needs further study.

SUMMARY

Indications of fruit-bud differentiation in the strawberry were found to extend over a considerable period before actual definite differentiation could be recognized.

Fruit-bud differentiation extended over a considerable period of time in some varieties; in others it occurred in a relatively short time.

Fruit-bud differentiation in all varieties and species studied under Maryland conditions, with one exception, was found to take place during September and early in October.

Fragaria nilgerrensis, a species native to northern India, did not differentiate fruit buds until November.

Rapidity and uniformity of subsequent development were found to vary to a considerable degree between the different varieties and species.

There is no absolute correlation between early differentiation of fruit buds, early blooming, and early ripening, or between late differentiation, late blooming, and late maturity. However, for many varieties this correlation actually existed.

FRUIT-BUD FORMATION IN EVERBEARING STRAWBERRIES [1]

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INTRODUCTION

In the northern part of the United States everbearing strawberries fruit in the spring, in the summer, and in the fall until freezing weather occurs. This habit of continuous bearing seems to be the result of certain environmental conditions in some cases and of genetic characteristics in others.

Since Goff [2] found that fruit-bud differentiation took place in the Clyde, a spring-bearing variety, in September, reports of subsequent investigations have been confined entirely to the spring-bearing varieties. This neglect of the everbearing strawberry is attributed to its comparatively recent appearance in this country and to the fact that it is as yet of little importance in the fruit industry. However, with the recent introduction of the Mastodon variety more interest promises to attach to the growing of this type of strawberry.

The studies reported in this paper were undertaken to determine how and when fruit-bud formation takes place in certain varieties of the everbearing strawberries.

MATERIALS AND METHODS

The investigations were conducted at East Lansing, Mich.,[3] during the summers of 1924 and 1925 and at the United States Plant Field Station, Glenndale, Md., during the spring months of 1926 and 1927. The work at East Lansing was confined entirely to the Progressive, an everbearing variety originated by Harlow Rockhill of Conrad, Iowa. The plants used at East Lansing were grown on a well-drained sandy soil. The studies at Glenndale included three varieties, all of which were originated by Rockhill. These plants were grown on a rich clay loam.

Crowns containing the buds for study were collected at intervals of 10 to 15 days throughout the experimental period in both localities. The usual methods of killing, fixing, and embedding as outlined by Chamberlain [4] were followed. Allowing the buds to remain in a 10 per cent hydrofluoric acid solution for about three days made sectioning much easier, because the acid dissolved the crystals of calcium oxalate, which greatly interfered with sectioning. The sections were mounted on slides, and photomicrographs and camera-lucida drawings were made of them.

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[1] Received for publication June 12, 1929; issued March, 1930.

[2] GOFF, E. S. INVESTIGATION OF FLOWER BUDS. Wis. Agr. Expt. Sta. Ann. Rpt. 17: 266-285, illus. 1900.

[3] The results of the investigations reported herein pertain to work performed at East Lansing, Mich., and done in partial fulfillment of the requirements for the degree of master of science at the Michigan State College, East Lansing, Mich.

[4] CHAMBERLAIN, C. J. METHODS IN PLANT HISTOLOGY. Rev. ed. 4, 349 p., illus. Chicago. [c1924.]

DEVELOPMENT OF THE CROWN

Vilmorin [5] says that the practical difference between the single and the perpetual-bearing strawberry can be traced back to an anatomical difference which consists in the production of flowering stems instead of runners from the axils of some of the leaves on the main stems. The investigations reported herein show that in the everbearing strawberry the growing point, which is located at the apex of the crown or runner, may differentiate into a fruit bud almost as soon as the elongating runner thickens into a crown, in some cases before roots appear. (Figs. 1, A and B.) However, a few leaves are usually produced in nearly all new-runner plants of everbearing strawberries before the growing point develops into a fruit bud. After a growing point of a crown has differentiated into an inflorescence there appears in the axils of many of the earlier formed leaves, possibly of all of them, meristematic tissue which may differentiate immediately into an inflorescence. However, there are usually a few or several leaves produced first which form a new crown. Sooner or later the growing point of this crown differentiates into an inflorescence, after which no further elongation of the crown can occur. Similarly, other crowns arise on those already developed, and thus in the course of time an old crown becomes very much branched, as is shown in Figures 4, C and D; 2, A, B, and C.

Everbearing strawberries produce a spring crop at about the same time that the spring-bearing kinds are fruiting. Following the spring crop there seems to be a period during which only a few ripe berries are produced. However, during this time, late May to early July, everbearers produce most of their runners. (Fig. 3.) Such everbearing varieties as Progressive, Rockhill, and Americus are not prolific runner producers. Apparently at the time the spring crop is ripe, or just following it, runners rather than branch crowns are developed in the axils of the leaves. Instead of the formation of only a few branch crowns and the production of runners in the axils of all the leaves, as occurs in the spring-bearing plants, many branches are formed and only a few runners are produced.

FRUIT-BUD DIFFERENTIATION

During the summers of 1925 and 1926, studies in Michigan showed that differentiation of fruit buds in the Progressive variety occurs throughout the summer. However, there was found to be a break in the continuous production of fruit; this break occurred immediately following the maturity of the spring crop. Before these observations were made the interrupted production between the spring crop and the summer and fall crop was assumed to be due to a corresponding break in the continuity of fruit-bud differentiation.

In order to determine how early in the spring fruit-bud differentiation takes place, studies were conducted at the United States Plant Field Station during the spring months of 1926 and 1927 with three varieties, Progressive, Rockhill, and Americus. Only a few early stages in fruit-bud formation were found until late in May. Those early stages which were found in April and early May may have been differentiated the previous fall. It seems apparent that a break

[5] VILMORIN, H. DE. PERPETUAL STRAWBERRIES. Roy. Hort. Soc. Jour. 22: 311-326, illus. 1898-99.

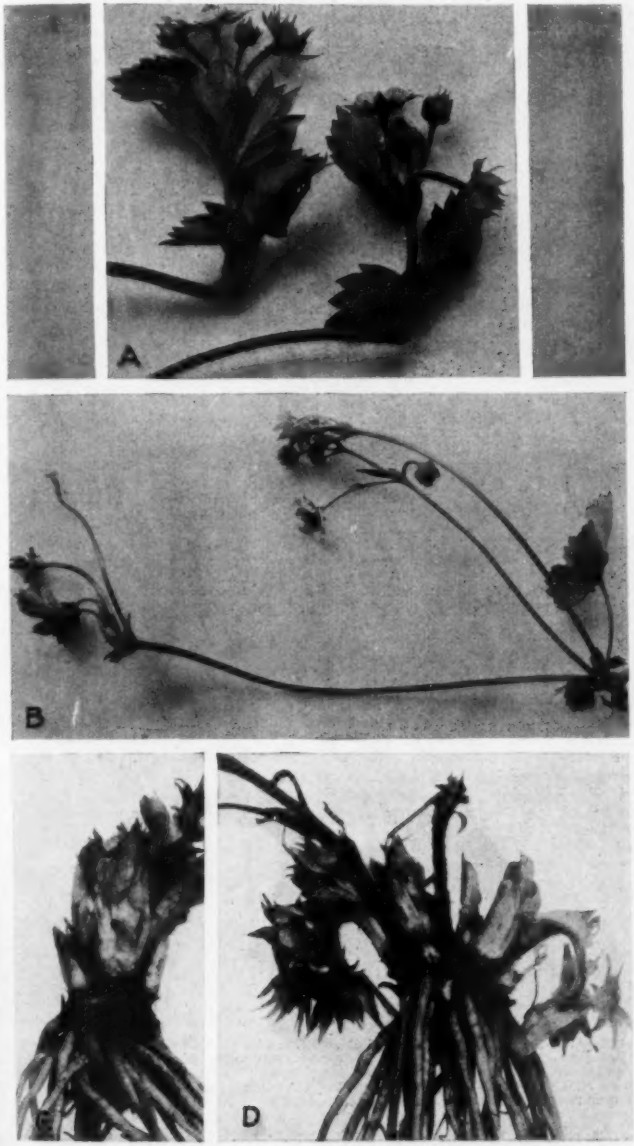

FIGURE 1.—A, Runner plants of U. S. D. A. No. 447 strawberry, with flowers open but no roots appearing. July, 1927. B, Runner plants of U. S. D. A. No. 400 strawberry beginning to take root and having flower stalks with open blossoms. July, 1927. C, Young plant of the Progressive strawberry, showing buds on the crown developing in the axils of the leaves, which have been removed. Photographed January 11, 1929. D, Runner plant of the Progressive strawberry which had taken root in June, 1928, showing old fruit stalks attached below the region where new branching is taking place. Photographed January 11, 1929

occurs in the continuity of fruit-bud differentiation in April and early May, a period when the fruit buds differentiated the previous fall are developing into fruit clusters. Figures 4, 5, and 6 show photomicro-

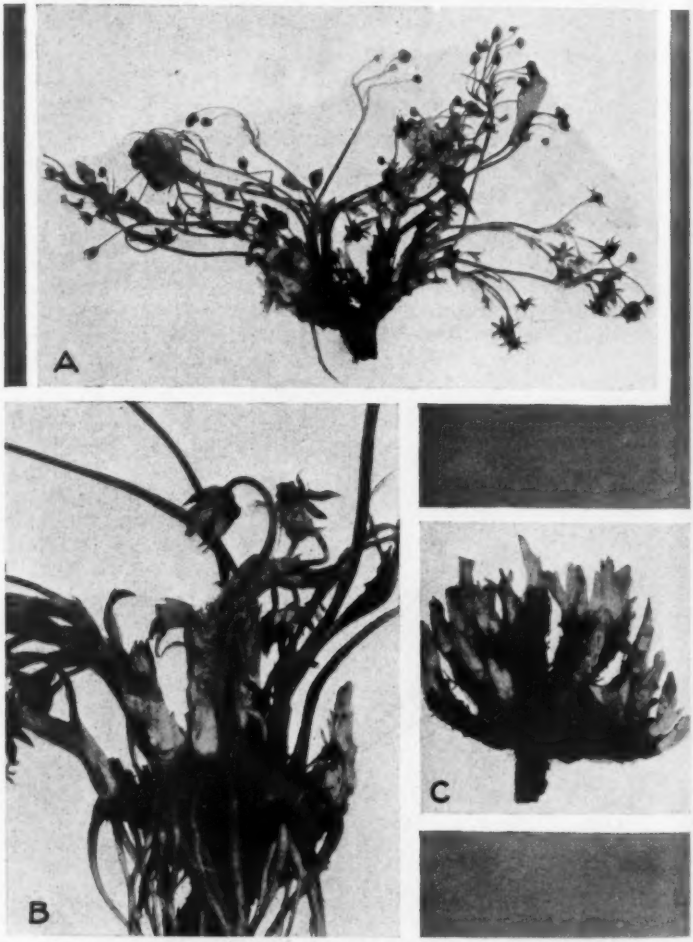

FIGURE 2.—A, Old plant of the Progressive strawberry, with old fruit stalks still attached. Photographed January 11, 1929. B, An old Progressive strawberry plant, showing old fruit stalks attached lower on the crown and new flower stalks terminating the new branches. Photographed January 11, 1929. C, Two-year-old Progressive strawberry plant from which leaves and roots have been removed in order to show the branched crown

graphs of the early stages in fruit-bud development, in both spring and fall, in the three varieties studied.

The fruit that ripens in May and early June develops from buds which apparently differentiated the previous fall, and the fruit that ripens in July develops from fruit buds differentiated late in May and

in June. Because of little or no differentiation in April, little or no fruit is produced in June and early July. Runner production is high during this time, but gradually becomes less, with fruit production increasing as the summer advances.

DISCUSSION AND SUMMARY

After producing a spring crop of fruit, strawberries of the everbearing type send out a few runners from the axils of their leaves. Instead of continuing runner production over an extended period, like the spring-fruiting type, everbearers may send out a flower stalk from

FIGURE 3.—A seedling clon of everbearing strawberry producing fruit buds on many runner plants and on some before they had rooted. July 13, Osage, Iowa

the leaf axil, though more often they produce very short branches, the growing point of each of which soon differentiates a fruit bud. As a result, fruit is produced throughout the summer from a crown which gradually becomes more and more branched, the process continuing until the cold of winter checks growth.

The almost entire absence of developing flower stalks over a period of three or four weeks immediately following the spring crop, together with the existence of favorable temperatures and long days, are suggested as the causes of the unusual activity of everbearing strawberries in producing runners, new branches, and differentiating fruit buds all at this time.

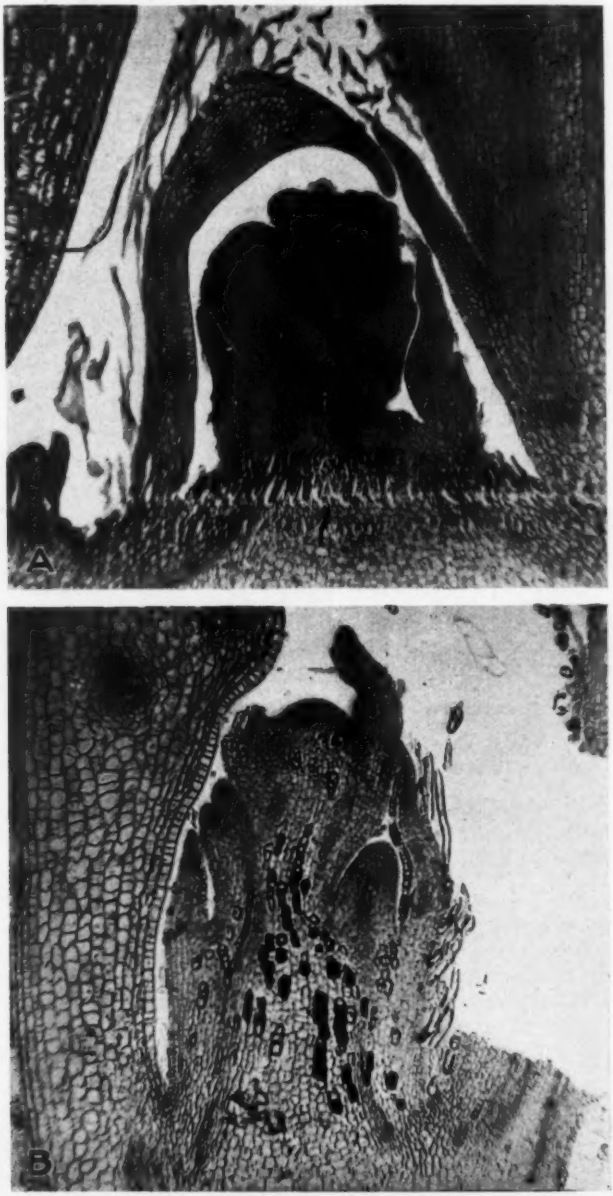

FIGURE 4.—A, Fruit bud of the Progressive strawberry, showing secondary flowers differentiating on May 25, 1926, at Glenndale, Md. B, Fruit bud of the Progressive strawberry in the process of differentiation on June 27, 1926, at Glenndale, Md. × 90

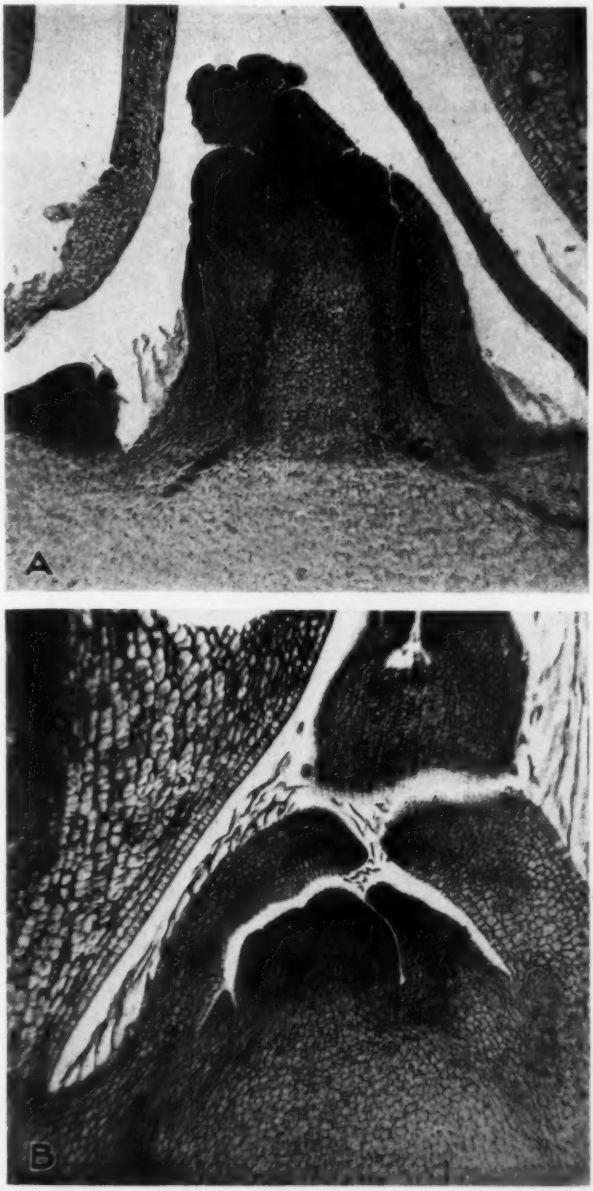

FIGURE 5.—A, Fruit bud of the Rockhill strawberry in process of differentiation on June 8, 1926, at Glenndale, Md. B, Fruit-bud differentiation just beginning in the Rockhill strawberry on October 7, 1926, at Glenndale, Md. × 90

FIGURE 6.—Fruit bud of the Americus strawberry, showing secondary as well as primary flowers in process of differentiation on June 8, 1926. × 90

EFFECT OF LEAF RUST (PUCCINIA TRITICINA ERIKS.) ON YIELD OF WHEAT[1]

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INTRODUCTION

The leaf rust of wheat (*Puccinia triticina* Eriks.) is more or less prevalent throughout the wheat-growing areas of the world. It very often so infects wheat that all the leaves and even the glumes are covered with uredinia. Opinions concerning the importance of this rust in wheat production, however, have varied considerably. Eriksson and Henning (*4*)[3] concluded that, in Sweden, leaf rust is rather innocuous because it occurs only on the leaves of its hosts. Carleton (*2, p. 40–41*) in the United States stated that—

> the orange leaf rust, as a rule, does very little, if any, damage to wheat, even during periods when it is quite abundant. * * * Occasionally, under certain conditions and in certain localities, considerable injury may ensue if the rust occurs much in advance of harvest.

McAlpine (*10, p. 64*), in 1906, reported "there are only two kinds of rust in wheat in Australia, the positively injurious *Puccinia graminis* and the comparatively harmless *P. triticina*, because it does not pinch and shrivel the grain like the other." However, in Australia, Cobb (*3*), in rust studies published from 1890 to 1894, recognized leaf rust as being destructive to wheat varieties commonly grown there at that time. According to Klebahn (*9*), leaf rust is one of the most prevalent diseases and occasionally most serious, causing much damage in the Province of Brandenburg, Germany. Grove (*5, p. 263*) stated that "the Brown Rust of Wheat [*P. triticina*] has been frequently so abundant in this country [Britain] in its uredo-stage as to cause great loss." Such statements are representative of the diverse opinions held by pathologists concerning the effect of the leaf rust on the yield of wheat.

In the United States, the Plant Disease Survey of the Bureau of Plant Industry, United States Department of Agriculture, was started in 1917 to obtain information concerning various plant diseases. In the summary of data on cereal crops, Haskell[4] made the following statements about leaf rust:

> The economic importance of this rust has been questioned by many pathologists. It is maintained that the affection of the leaves, coming on rather late in the

[1] Received for publication July 24, 1929; issued March, 1930. Published with the approval of the director as a contribution from the department of botany, Purdue University Agricultural Experiment Station, La Fayette, Ind. Cooperative investigations between the Purdue University Agricultural Experiment Station and the Office of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture.

[2] The writer wishes to express his thanks to C. R. Ball and H. B. Humphrey, of the Office of Cereal Crops and Diseases, for many helpful suggestions and criticisms, and his appreciation of the assistance rendered by Miss Dorothy M. Thompson and Leroy E. Compton in the course of these investigations.

[3] Italic numbers in parentheses refer to "Literature cited," p. 446.

[4] HASKELL, R. J. SUMMARY OF PLANT DISEASES IN THE UNITED STATES IN 1918. IV. DISEASES OF CEREALS AND FORAGE CROPS. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bul. Sup. 4: 119–159, illus. 1919. [Mimeographed.] (See p. 131.)

season, as it usually does, does not materially reduce the size or number of kernels. After the kernels are well formed it is said that the leaves are not necessary for full development of the grain so long as the culms remain green. In 1917, collaborators were asked in a questionnaire if they considered the disease of economic importance and replies from Pennsylvania, Maryland, North Carolina, South Carolina, Tennessee, and Indiana were in the affirmative. Collaborators in most of the other States indicated that usually it was not of importance. In Oregon it was said to be of importance on certain varieties only.

Melchers (*12*) reported that in Kansas, during 1917, leaf rust was abundant and that careful observation indicated that no other factor could be responsible for the poor quality and low yields. The yield of one field was reduced 38 per cent.

In 1918, an investigation of the leaf rust of wheat was started as a cooperative project between the Purdue University Agricultural Experiment Station and the Office of Cereal Crops and Diseases of the Bureau of Plant Industry, United States Department of Agriculture. On account of the differences in opinion and the lack of accurate information concerning the effect of leaf rust on the yield of wheat, a series of experiments for the purpose of comparing rusted and rust-free wheat was started in 1921 as one phase of the investigation.

EFFECT ON SUSCEPTIBLE VARIETIES

GREENHOUSE STUDIES

In 1921, Red Fern, a spring wheat, and Mediterranean, a winter wheat, both very susceptible to leaf rust, were used. They were grown in the greenhouse at the Purdue University Agricultural Experiment Station in 6-inch pots, one plant to a pot. Six plants of Red Fern and five of Mediterranean were inoculated 40 days after planting, when the tillers were well developed. An equal number of plants were left uninoculated as checks (C). The resulting infection of the inoculated [5] plants was slight, averaging 15 per cent for Red Fern and 10 per cent for Mediterranean. These infection percentages represent the actual amount of infection compared with the amount possible. No infection occurred on the check plants. The rusted series were reinoculated at intervals of 25, 18, 16, 17, and 24 days with average infections of 15, 30, 40, 65, and 85 per cent resulting. The maximum infection was obtained when the plants were slightly past blossoming. A slight infection developed on the checks, reaching 35 per cent following blossoming.

The plants of the rusted series (R) were slightly stunted (fig. 1) and developed more tillers than the checks (C). Many tillers of the rusted plants (R), however, did not develop heads, and the heads produced were somewhat later in maturing than those of the checks (C).

The heads of each plant were harvested and threshed separately. Table 1 gives the results obtained. The rusted plants of Red Fern produced 15.5 per cent fewer heads than the checks, while Mediterranean showed a reduction of 12.1 per cent. There also was a decided reduction in the number of kernels per head. Red Fern averaged 7.9 kernels per head for the rusted compared with 12.1 for the checks. Mediterranean averaged 8.8 kernels for the rusted compared with 15.7 for the checks. While a large part of the reduction in yield was due to the fewer kernels produced, a portion was due to reduction in weight of the kernels, as is shown by the average weight per kernel.

[5] Throughout this paper such inoculated series are referred to as the rusted series (R).

In both the check and the rusted plants the grain showed shriveling. While practically all the grain from the rusted plants was shriveled, the check plants showed 43 per cent of shriveled kernels.

In this experiment, the plants were infected only slightly to moderately during their earlier development. Even after heading, the

FIGURE 1.—Plants of Red Fern wheat: A, Moderately rusted from tillering to maturity and showing stunting and fewer heads than B, which is slightly rusted

infection never reached 100 per cent. Some infection, however, occurred during a considerable portion of the development. Such a condition probably seldom occurs in the field in the northern part of the United States, but in the South such a development of rust may occur occasionally.

TABLE 1.—*Effect of infections of various intensities and durations by the leaf rust on yield of wheat in the field and in the greenhouse at La Fayette, Ind.*

[The capital letters in column 3 indicate different treatments discussed in the text. T=trace]

Year	Variety	Treatment	Amount of rust [a]	Stage of growth	Units	Heads	Kernels	Average kernels per unit	Reduction in number of kernels	Yield (total)	Average	Reduction in weight	Average weight per kernel
			P. ct.		*No.*	*No.*	*No.*	*No.*	*P. ct.*	*Gm.*	*Gm.*	*P. ct.*	*Mg.*
1921	Red Fern	C	0-35	Tillering	[b] 6	71	862	143.66 ±13.5		24.3	4.05 ±0.38		28.3
1921	do	R	15-85	do	[b] 6	60	475	79.16 ±13.24	44.9	10.4	1.73 ±.34	57.2	21.9
1921	Mediterranean	C	0-35	do	[b] 5	74	1,164	232.8 ±16.53		26.7	5.35 ±.053		22.9
1921	do	R	10-85	do	[b] 5	65	576	115.2 ±14.0	50.5	9.6	1.92 ±.286	63.3	16.7
1922	Fulcaster	CA	0-5	Heading	[c] 12	83	3,883	323.6 ±21.85		139.5	11.6 ±.736		35.9
1922	do	RB	75-100	Tillering	[c] 6	4	90	15.0 ±2.54	95.4	1.9	.32 ±.096	97.4	21.1
1922	do	RC	50-100	Shooting–	[c] 12	13	409	34.1 ±7.61	89.5	12.3	1.02 ±.196	91.3	30.1
1922	do	RD	100	Boot–	[c] 9	53	1,342	149.1 ±.52	53.9	47.9	5.32 ±.189	54.3	35.6
1923	do	C	0-5	Blossoming	[d] 38	99				73.76	1.94		
1923	do	R	75-100	do	[d] 48	121				70.12	1.46	24.7	
1925	Michigan Amber	C	0-1	do	[e] 8	239	2,515	314.37 ±14.61		90.18	11.27 ±.513		35.8
1925	do	R	100	do	[e] 8	234	2,009	251.37 ±14.07	20.1	59.88	7.48 ±.434	33.5	29.8
1927	do	CA	0-1	Boot+	[f] 15	95	2,183	145.5 ±4.76		72.14	4.81 ±.173		33.0
1927	do	RA	75-100	do	[f] 15	95	1,910	127.3 ±5.09	12.5	45.31	3.02 ±0.73	37.2	23.7
1927	do	CB	0-T	Blossoming	[e] 5	241	3,285			120.39	24.08 ±1.03		36.6
1927	do	RB	90-100	do	[e] 5	246	2,963		9.8	87.68	17.54 ±0.56	27.2	29.6
1927	Illinois No. 1	CC	75-100	Ripening	[g] 80					11,967.0	149.5 ±2.09	24.2	
1927	do [h]	DC	T-35	do	[g] 80					15,794.0	197.4 ±3.18		
1927	do [h]	CD	75-100	do	[i] 150	3,681		24.5 ±.46	18.9	101.1		25.8	27.5
1927	do [g]	DD	T-35	do	[i] 150	4,538		29.9 ±.49		136.3			30.0
1927	Trumbull	CE	75-100	do	[g] 80					22,742.0	284.3 ±3.38	11.1	
1927	do [h]	DE	T-35	do	[g] 80					25,575.0	319.7 ±3.66		

[a] The minimum rust intensity occurred at the stage given in column 5 and developed later to the maximum.
[b] Number of pots; one plant grown in a 6-inch pot.
[c] Number of pots; four plants grown in a 6-inch pot.
[d] Number of plants.
[e] Number of rows in the greenhouse bench.
[f] Number of pots; two plants in each rusted and two as checks.
[g] Number of rod rows in field plots.
[h] Rod rows in field plots dusted with sulphur to prevent rust development.
[i] Sample of 150 heads selected from dusted and rusted plots.

In 1922 an experiment was conducted to determine the effect of leaf-rust infection at different stages of development. A strain of Fulcaster (C. I.[6] No. 4892), very susceptible to leaf rust, was used. Four plants were grown in each 6-inch pot in order more nearly to approach field conditions. The pots of wheat were divided into four lots. Lot A, comprising 12 pots, was used as check. (CA, Table 1.) A slight infection, about 5 per cent, developed following heading. Lots B, C, and D were rusted plants. (RB, RC, and RD, Table 1.)

[6] C. I. indicates accession number, Office of Cereal Crops and Diseases.

Plants of lot B, consisting of 6 pots, were inoculated as soon as they were well tillered. The infection was severe, averaging 75 per cent. The plants of this lot were reinoculated at intervals as new leaves developed, and an infection of 100 per cent was maintained for most of the development of the plants. Plants of lot C, consisting of 12 pots, were inoculated when they were starting to shoot. The initial infection was 50 per cent. These plants were reinoculated at intervals and an infection of 100 per cent was obtained and maintained to maturity. Plants of lot D, consisting of 9 pots, were inoculated when the first indication of heading was evident. At this time all the leaves were practically fully developed. An infection of 100 per cent was obtained.

Table 1 also gives the effects on yield for 1922 in lots A to D of Fulcaster wheat. The early infections of lots B and C resulted in a marked reduction in the number of heads developed. While the check pots averaged 6.9 heads per pot, lot B averaged only 0.6 and lot C only 1.1 heads per pot. Lot D, inoculated when the heads were showing in the boot, averaged 5.9 heads. The plants subjected to the earlier infections were stunted. Even those culms which produced heads were shorter than those of the check plants. The lower leaves of the rusted plants also died considerably in advance of those of the check. There was very little difference in height between the late-infected (lot D) and the check plants. The leaves of the rusted plants, however, died more rapidly than those of the check. Ten days following inoculation, when uredinia were just showing, the upper three leaves of the rusted plants were green and the lower two were yellowish and dying at the tips. The corresponding five leaves of the check plants were entirely green. Thirteen days later the two upper leaves of both the rusted and the check plants were still green. About one-half of each of the next two lower leaves of the rusted plants was dead, while only the tips of the corresponding leaves of the check plants showed indications of dying. The lower leaves of the rusted plants were entirely dead, while the terminal halves of those of the check plants were yellowish. Thirteen days later only the basal portions of the two upper leaves of the rusted plants were still green and the three lower leaves were entirely dead. Except for the tips, which were yellowish or dying, the three upper leaves of the check plants were green. From one-third to seven-eighths of each of the two lower leaves was yellowish or dead. Six days later all the leaves of the rusted plants were dead, but the upper leaf of the check plants was green and about one-eighth to one-half of each of the lower leaves still showed green tissue. The plants were mature 10 days later.

The straw from the 12 check pots weighed 438.5 gm., an average of 36.5 gm. per pot. The straw from the 6 pots of early-inoculated wheat (lot B) weighed 64.5 gm., or an average of 10.7 gm. per pot and a reduction of 70.6 per cent. The straw from the 12 pots of the next inoculation (lot C) weighed 120.5 gm., an average of 10 gm. per pot and a reduction of 72.6 per cent. The straw from the 9 pots of the late inoculation (lot D) weighed 219.7 gm., an average of 24.4 gm. per pot and a reduction of 33.1 per cent.

The grain produced by the earlier infected plants (lots B and C), was not so plump as that produced by the check plants, as is shown by the average weight per kernel in Table 1. The early-inoculated lot (B) had 71.4 per cent of shriveled kernels and the next lot (C) had

71.7 per cent, as compared with 20.2 per cent in the case of the check plants. The late-inoculated lot (D) produced kernels of practically the same average weight as those produced by the check plants and contained fewer (13 per cent) shriveled kernels, because a large number of shriveled kernels had been produced by one plant of the check.

The early infections exerted a very pronounced effect upon the development of the wheat plant. The large losses in yield were due to a reduction in the number of heads and kernels produced, although the average weight per kernel also decreased very markedly. Late infection brought about a reduction in yield largely by reducing the number of kernels produced. There was also some reduction in weight per kernel, which, however, is obscured by the shriveling in one of the check plants.

In 1923 an experiment was conducted in which Fulcaster wheat was inoculated still later in its development. The results are shown in Table 1. Thirty pots were sown with the Fulcaster variety. Four plants were grown in each pot. Plants in half of the pots were inoculated (R) with rust when the heads had started to blossom. An infection of 75 to 100 per cent was obtained. The check plants (C) developed a slight amount of rust (5 per cent) in some cases. Unfortunately, sparrows entered the greenhouse when the plants were about ready to harvest and ruined part of the plants. These were eliminated from the experiment, and the yield, consequently, is based upon the average yield per plant, rather than per pot as in previous years. On account of lack of assistance, the plants were not harvested separately, and the kernels were not counted. The average number of heads per plant in the check pots was 2.6 and in the rusted 2.5. As the plants were not inoculated until the heads were in bloom, no effect on head production was to be expected. The reduction in yield, although still considerable, was much less than when infection took place earlier.

In 1924 a similar experiment was undertaken. Mildew developed on the plants during the winter, however, and the experiment was discontinued.

In 1925 a strain (29–1–1–1) of the Michigan Amber variety, which had been found resistant to powdery mildew (*Erysiphe graminis*) and highly susceptible to leaf rust, was used. In order to approach field conditions as closely as possible, the wheat was sown in rows in the greenhouse bed. Sixteen 5-foot rows were spaced 6 inches apart, and the kernels were dropped approximately 1 inch apart in the rows. The soil was ordinary well-mixed field soil taken from plots back of the experiment station. The plants were inoculated on April 17, when the heads were well developed and in early bloom. The rows were covered with a muslin cage with a partition separating them into two series of 8 rows each. Each series was heavily atomized, and one (R) was thoroughly dusted with urediniospores of leaf rust by shaking heavily rusted plants over them. The other series of eight rows was left uninoculated. The muslin cover over each cage was then thoroughly wet. The inoculation was made in the late afternoon, and the next morning all covers were removed. Uredinia were first noted on the sixth day, and in 10 days an infection of 100 per cent had developed on the inoculated plants (R). The check (C) rows showed no rust at this time. Although care was taken in watering to prevent wetting the foliage, a slight infection of about 1 per cent developed

before maturity on the lower leaves of the plants in the check rows. On May 20, 33 days after inoculation, only the upper or flag leaf of the infected plants was still alive. The check plants had two or three of the upper leaves green and in good condition. A week later when the heads of both rusted and check plants were showing signs of ripening, all the leaves of the rusted plants were dead, while one or two upper leaves of the checks were still in a good condition. The rows were all harvested on June 6. A few of the flag leaves of the check lots were still partly green, although the heads were ripe.

On account of the difficulty of separating the material by plants, the wheat was harvested by rows. There was practically no difference in the number of heads produced. (Table 1, 1925.) Most of the reduction in yield was due to the fact that fewer seeds were produced by the rusted plants, although there was also a reduction in the average weight of the kernels. There was very little shriveling, the check having about 3.1 per cent, and the rusted plants a little over twice as much, or 7.7 per cent of shriveled kernels.

In 1926 the previous experiment was repeated, using a heavily fertilized soil (greenhouse compost). During the winter the growth was so rank that considerable lodging and irregular overshadowing and development occurred. It was evident that the rows could not be divided in a comparable way, and the experiment was discontinued.

In 1927 studies were made in the greenhouse with wheat in pots (A) and in rows in the bench (B). Fifteen 6-inch pots, each containing four plants of Michigan Amber (29–1–1–1), were used in the pot experiment. The plants were inoculated when the heads were just emerging from the boot. In order to reduce as much as possible the variation due to differences in environmental conditions, each pot was divided into two parts with muslin, each part containing two plants. Two of the plants of each pot were inoculated on May 1 (RA, Table 1), and the other two served as checks (CA, Table 1). Twelve days later the inoculated plants showed 75 to 100 per cent of rust. The check plants showed an occasional uredinium, and before maturity about 5 per cent of rust had developed on the lower leaves, representing an average of 1 per cent for the whole plant in the checks. At this time the uppermost leaf of each infected plant was slightly yellowish at the tip, while the three leaves below were entirely yellowish green. The three upper leaves of the check plants were green and one leaf below was yellowish. Twelve days later (May 24) the flag leaves of the infected plants were yellowish green and all the other leaves were dead. The three upper leaves of the check plants were green and the next ones below were dead. Fourteen days later (June 7) all the leaves of the infected plants were dead, the heads were nearly all ripe, and the straw was yellow. A few of the flag leaves of the check plants were yellowish green, while the rest were dead. Most of the heads were ripe. The straw showed a decided purpling.

Both the rusted plants and the check plants had the same number of heads. (CA and RA, Table 1, 1927.) However, there was not only a decided reduction in the number of kernels produced (12.5 per cent), but also considerable of the reduction in yield was due to a decrease in weight of the kernels, as is shown by a comparison of the average weights per kernel.

In 1927 the Michigan Amber variety (29–1–1–1) was sown also in the greenhouse bench in rows 4 feet long and 6 inches apart. The

seeds were spaced about an inch apart in the row. The plants were inoculated when the heads were fully developed and after blossoming had started. As in 1925, the rows were divided into two groups of 5 rows each by muslin cages, when they were inoculated. Five rows were inoculated (RB) and five served as checks (CB).

Fifteen days following inoculation the plants in the inoculated rows showed 90 to 100 per cent of rust. The check plants showed no infection to a trace. Twenty-seven days after inoculation the flag leaves of the infected plants were still alive, although slightly yellowish green; the other leaves were dead, except for an occasional leaf just below the flag leaf, which was still alive but yellow. At this time the two upper leaves of the check plants were entirely green, the third leaf from the top was yellowing at the tip, and the lower leaves were dead. Thirty-eight days after inoculation practically all of the infected leaves were dead. The stalks and heads of the infected plants were yellowing. The upper leaves of the check plants were about half green, the heads were yellowish, and the stalks were a pronounced purple. Nine days later both the rusted and the check plants were ripe. The straw of the rusted plants was a dull yellow, while that of the checks plants showed considerable purpling.

There was practically no difference in the number of heads produced by the rusted (RB) and check (CB) rows. (Table 1, 1927.) While part of the reduction in yield was due to the fewer kernels produced by rusted plants, most of it was brought about by reduction in weight per kernel. Although part of this was due to an increased production of shriveled kernels, 3.1 per cent in the check and 8.6 per cent in the rusted plants, most of it may be accounted for by the fact that the kernels were slightly smaller and consequently lighter. There was considerably more yellow berry in the grain from rusted plants, 32.8 per cent for the rusted as compared with 16.4 per cent for the check plants. The weight of the air-dried straw from the five check rows was 305 gm. and from the rusted rows 270 gm., a reduction of 11.4 per cent.

FIELD STUDIES

Sulphur has proved to be a very effective fungicide for preventing the germination of urediniospores of the leaf rusts.[7] Kightlinger (*7*) has reported experiments showing that sulphur applied as a dust was effective in controlling crown rust of oats in the field. Kightlinger and Whetzel(*8*) and Bailey and Greaney (*1*) reported the successful use of sulphur dust to control leaf rust of wheat in the field.

During 1925 and 1926, attempts were made to obtain data on losses produced by leaf rust under field conditions. The use of sulphur fungicides as sprays and dusts resulted unsuccessfully because of the slight amount of rust present in the experiment station plots in both years.

In 1927 two varieties of wheat—Trumbull, a winter wheat, and Illinois No. 1, a spring wheat—were sown on the agronomy farm at La Fayette, Ind., where leaf-rust epidemics are more certain to occur. Each variety was sown in twenty-five 18-foot rows, 1 foot apart, in each of eight plots. Each plot was sown as follows: 1 row for border;

[7] Data obtained in studies for the degree of master of science in agriculture in the department of botany, Purdue University Agricultural Experiment Station, and presented, in an unpublished thesis, by Leroy E. Compton, assistant pathologist, Office of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture, 1926.

10 rows dusted with sulphur (Kolodust); 3 rows to serve as protection against dust drift; 10 rows not dusted; 1 row of border. This provided eight 10-row plots for dusting and eight 10-row plots not dusted for each variety, besides guard and separation rows.

The spring variety, Illinois No. 1, was dusted six times between May 25 and July 5. Leaf rust was first noted on May 31, when the plants were shooting. At this time a trace of rust occurred on the undusted rusted check plants and none on the dusted ones. On June 23 the plants of this variety were blossoming, and 25 to 50 per cent of rust occurred on the undusted rusted checks and a trace to 5 per cent on the dusted plants. On July 8 the kernels were about two-thirds formed and 50 to 100 per cent of rust had developed on the undusted rusted checks (Table 1, 1927, CC) and a trace to 35 per cent on the dusted plots (DC). On July 16 the wheat was ripening and the undusted rusted checks showed 75 to 100 per cent of rust (CC) and the dusted still a trace to 35 per cent (DC).

Leaf rust became destructive on Illinois No. 1 at an earlier stage in its development than in the case of Trumbull. A moderate to heavy infection from blossoming to maturity resulted in an average yield of only 149.5 gm. per row, or 14.95 bushels per acre, from the undusted and rusted checks (Table 1, 1927, CC), whereas the dusted plots produced an average yield of 197.4 gm. per row, or 19.74 bushels per acre (Table 1, 1927, DC). The reduction caused by rust was 4.79 bushels per acre, or 24.2 per cent.

A sample of 150 heads was selected at random from both the undusted and rusted checks and the dusted plots of Illinois No. 1. These heads were carefully threshed by hand, and the kernels were counted for each head. As shown in Table 1 (1927, CD and DD), the total reduction in yield agreed rather closely with that in the yield from the entire eight 10-row plots (Table 1, CC and DC). This study shows that the reduction in yield was due largely to the fact that the undusted and rusted plants produced fewer kernels.

The Trumbull winter wheat (fig. 2) was given five dustings between May 25 and June 27. On May 31 the wheat was in head, and a trace to 10 per cent of rust was noted in the undusted check plots, while none was present in the dusted plots. On June 23 the wheat was considerably past blossoming, and 50 to 100 per cent of rust had developed on the undusted rusted checks, whereas only a trace to 10 per cent occurred on the dusted plots. (Fig. 2.) At that time practically all of the lower leaves of the rusted plants were dead and the upper leaves were yellowish. Most of the lower leaves of the dusted plants were dead, but the upper ones were still green. On June 29 the wheat was ripening and the undusted rusted check plants showed 75 to 100 per cent of rust (Table 1, 1927, CE) and the dusted a trace to 35 per cent (Table 1, 1927, DE). All the leaves of the rusted plants were dead. Most of the upper leaves of the dusted plants were still alive but were yellowish. Both undusted and dusted plots were harvested July 5, a foot being trimmed from each end of the rows and the yield obtained in grams for a 16-foot row.

The rust on Trumbull did not become severe until it was well past blossoming, and it reached a maximum only a short time before maturity. The average yield of the undusted rusted check plots was 284.3 gm. per row, or 28.43 bushels per acre (Table 1, 1927, CE),

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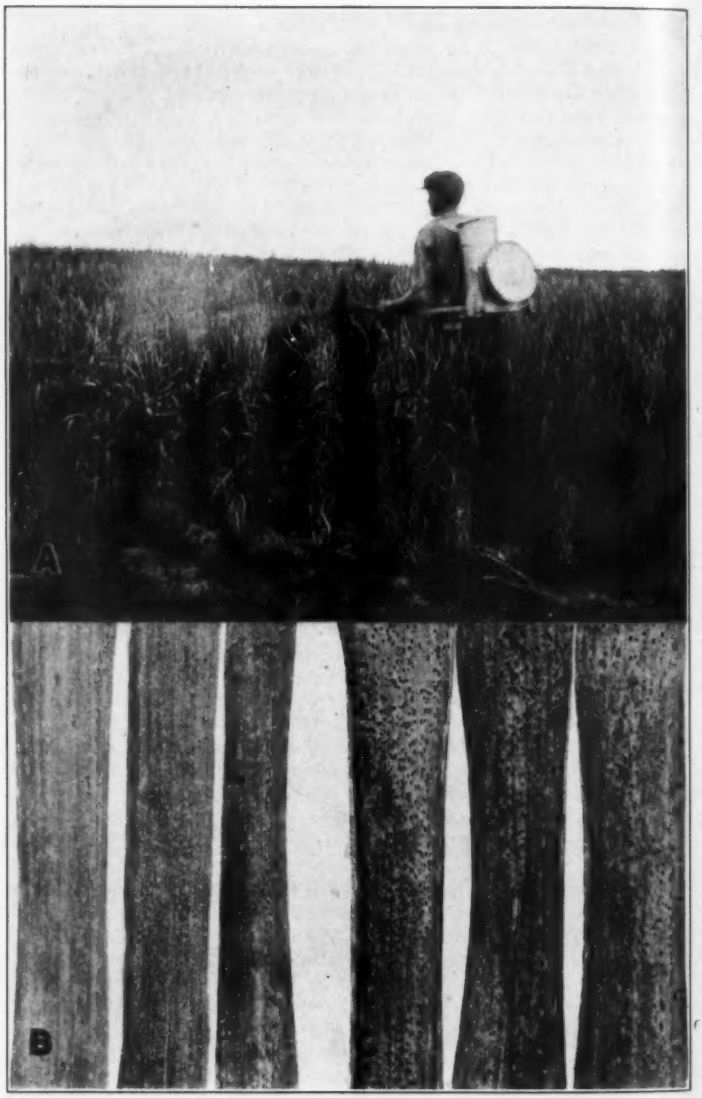

FIGURE 2.—A, Dusting plots of Trumbull wheat with sulphur to control leaf rust; B, three clean leaves from sulphur-dusted plots; C, three rusted leaves from plots not dusted and heavily rusted

whereas the average of the dusted plots was 319.7 gm. per row, which is equivalent to 31.97 bushels per acre (1927, DE). The reduction in yield was 3.54 bushels, or 11.1 per cent.

As is evident, the rust was able to develop on the undusted plants to a considerable extent, while it was largely prevented from developing on those which were dusted. The former, therefore, are comparable to the rusted plants in the greenhouse studies, and the latter serve as checks in a comparison of the effects of the rust upon yield.

EFFECT ON A RESISTANT VARIETY

During the winter of 1926–27 a study was made in the greenhouse to determine the effect of infection on a resistant variety. Ten pots of the Webster variety (C. I. 3780), four plants to a pot, were used in the greenhouse in a manner similar to that employed with Michigan Amber. Webster is very resistant to physiologic form 5, which was used for inoculation (*11*). On May 1, two plants of each pot were inoculated. At this time the heads were just emerging from the boot. On May 12 infection was indicated on the inoculated plants by numerous small necrotic flecks. Approximately as much infection occurred as in the susceptible Michigan Amber (Table 1, 1927, CA and RA), but the infected cells of the host were soon killed and the rust did not sporulate. The flag leaf was green and apparently in good condition. The two leaves next below showed considerable yellowing. The next lower leaf was dead. On the check plants the three upper leaves were in good condition. The fourth leaf from the top showed considerable yellowing. On May 24 virtually all the leaves of the inoculated plants were dead. The two upper leaves of the check plants were green, the third leaf from the top was yellow and dying, and the fourth was dead. On June 7 the rusted plants were ripe, while the check plants still showed a slight amount of green color in the leaves. The heads and kernels were apparently mature.

All the plants were ripe on June 15 and were then harvested. The 20 check plants produced 1,040 kernels, weighing 41.32 gm., while the rusted ones yielded 1,130 kernels, weighing 36.58 gm. On the basis of total production, the rusted plants showed an increase of 8.6 per cent in number of kernels. However, it is evident that infection had a decided effect on the weight of grain, the total yield of the infected plants being reduced 11.4 per cent. The average weight per kernel from the check plants was 39.6 mg. and from the rusted plants 32.3 mg. The reduction in yield for the correspondingly inoculated susceptible Michigan Amber was 37.2 per cent.

From this one experiment it would appear that the infection of resistant varieties may result in a decided reduction in yield, the effect being largely produced by a reduction in size and weight of the kernels.

EFFECT ON KERNEL FORMATION

As can be seen from Table 1, the reduced yield resulting from rust infection was due in part to the production of fewer kernels and in part to a reduction in the weight of the individual kernels. A study of the number of kernels produced per spikelet by rusted plants and by check plants, respectively, was made to determine in what part of the head the reduction in number occurred. The heads from a representative sample of both rusted and check plants were threshed by

hand. The number of kernels for each spikelet in each head was recorded, as well as the position of the spikelet in the head. In this way 21,769 spikelets from 1,331 heads were studied (Table 2) from material obtained during the four years of the investigation, 1921, 1922, 1925, and 1927.

TABLE 2.—*Effect of the leaf rust of wheat on the number of kernels produced per spikelet*

[See Table 1 for rust intensities and duration]

Year	Variety	Condition of plant	Number of heads	Number of spikelets producing—						Total kernels
				0 kernel	1 kernel	2 kernels	3 kernels	4 kernels	5 kernels	
1921	Mediterranean	Check	74	614	435	348	11	0	0	1,164
		Rusted	65	724	318	129	0	0	0	576
1922	Fulcaster	Check	47	293	132	242	288	101	5	1,909
		Rusted	47	554	134	142	115	16	2	837
1925	Michigan Amber	Check	59	376	212	238	19	0	0	748
		Rusted	62	406	202	183	18	0	0	622
1927	do	Check A	95	615	286	547	259	4	2	2,183
		Rusted A	95	676	383	583	119	1	0	1,910
1927	do	Check B	241	1,645	668	825	293	22	0	3,285
		Rusted B	246	1,768	719	888	156	0	0	2,963
1927	Illinois No. 1	Dusted	150	478	372	1,219	540	27	0	4,538
		Rusted	150	498	437	1,208	268	6	0	3,681

In 1921 all the heads of both rusted and check plants of Mediterranean wheat were studied. As shown in Table 2, the 74 heads of the check plants had 11 spikelets each containing three kernels, whereas in the 65 heads from the rusted plants there was no spikelet that produced three kernels. The heads from the checks averaged 4.7 spikelets and the heads of the rusted plants 1.98 spikelets producing two kernels; the former had an average of 5.9 and the latter plants 4.9 spikelets producing one kernel. The heads of the check plants had an average of 8.3 spikelets and those of the rusted 11.1 spikelets producing no kernels. There was a pronounced increase, therefore, in the number of sterile spikelets in the rusted plants. These were located mostly in the upper and lower portions of the heads. The spikelets of the check plants containing three kernels were located in the central part of the head. The majority of spikelets of the rusted plants containing two kernels were found in the central part of the heads, while in the check plants those containing two kernels were more generally distributed.

In 1922, 47 heads from the check plants and 47 from the late-inoculated plants of Fulcaster were similarly studied. The results (Table 2) agree with those of 1921. The contrast in the numbers of spikelets producing four kernels is especially noticeable, 101 in the checks as compared with 16 in the rusted plants. An additional study of the effect of rust on the development of kernels in different parts of the head was made on a portion of this material.

The location of the kernels in the heads of Fulcaster wheat is illustrated in Table 3 and Figure 3. The numbers of kernels per spikelet are given as they were arranged in 10 heads each from the rusted

and from the check plants. Spikelets producing four kernels are common in the central part of the heads from check plants, while none developed in the rusted ones. Spikelets producing three kernels were found in the upper and lower portions of the heads of the check plants but were restricted largely to the central portion of the heads of the rusted. A much larger number of sterile spikelets occurred in

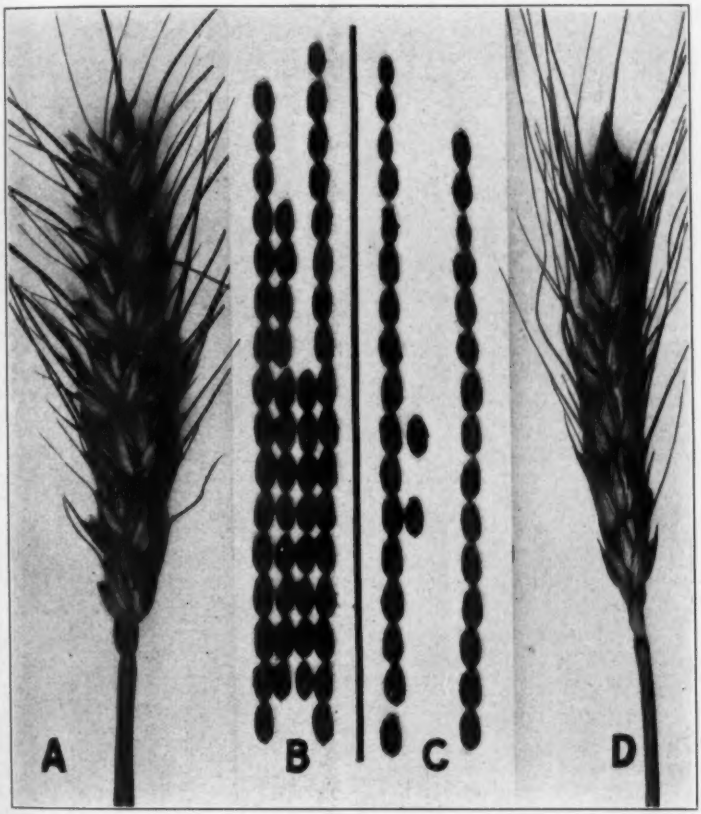

FIGURE 3.—Effect of leaf rust on the number of kernels per spikelet of Fulcaster wheat in relation to their position on the head: A, Head from check plant (C); B, kernels of each spikelet from A arranged as they occurred in the spikelet; C, kernels of each spikelet from D arranged as they occurred in the spikelet; D, head from a rusted plant (R). The plants from which C was selected were rusted 100 per cent while the heads were still in the boot

the upper and lower portions of the heads of the rusted than in those of the check plants.

In 1927 similar studies were made of heads from rusted and check plants of Michigan Amber wheat in the greenhouse. Michigan Amber usually does not produce so many kernels per spikelet as Fulcaster. The first series studied consisted of heads from pots in which two of the four plants were inoculated and rusted and two were not inoculated and nearly rust free. In the rusted plants there was a

decided reduction in the number of spikelets producing three kernels, as is shown in Table 2 (1927, A). Here, again, the spikelets producing three kernels were more generally distributed throughout the heads of the check plants and more narrowly limited to the central portion of the heads of the rusted plants. The sterile spikelets were somewhat more numerous in the upper and lower portions of the heads of the rusted plants, but the difference was not so noticeable as in the case of the earlier inoculated Fulcaster.

TABLE 3.—*The number of kernels per spikelet in relation to position in heads of rusted and check plants of Fulcaster wheat grown in the greenhouse at La Fayette, Ind., in 1922* [a]

Arrangement of spikelets [b]	Heads from rusted plants											Heads from check plants									
	Number of kernels per spikelet in head—										Total kernels	Number of kernels per spikelet in head—									Total kernels
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10		No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10	
M′	0	0	---	---	---	---	---	---	---	---	0	---	0	---	---	---	---	1	---	---	---	1
L′	0	0	---	---	---	---	---	---	---	---	0	0	0	0	0	0	0	2	---	---	---	2
K′	0	0	0	0	0	---	0	0	---	---	0	1	0	0	0	0	0	1	---	0	0	2
J′	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	4
I′	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	2	2	1	0	1	8
H′	1	0	0	0	0	0	0	0	0	0	1	1	0	2	0	2	1	2	1	1	1	11
G′	1	1	1	0	0	0	0	0	0	0	3	2	3	2	3	2	2	3	2	1	2	22
F′	1	1	2	0	0	0	0	0	0	0	4	2	2	2	3	2	2	3	2	1	2	21
E′	2	2	2	1	0	0	2	0	0	0	9	3	3	3	3	1	2	3	2	2	2	24
D′	2	2	2	2	1	2	0	0	0	---	13	3	3	3	3	3	3	3	2	2	2	27
C′	2	2	2	2	2	2	2	0	1	0	15	3	4	3	4	3	3	3	3	1	2	29
B′	2	2	3	2	2	2	2	0	1	0	16	3	4	3	4	3	3	4	3	2	3	32
A′	3	2	2	2	3	2	2	1	1	0	18	4	4	4	4	3	3	4	3	2	3	34
A	3	2	3	3	3	1	1	1	2	0	19	4	3	4	4	2	3	4	3	2	3	32
B	3	3	3	2	3	1	2	3	1	0	21	4	4	4	4	3	3	4	3	2	3	34
C	3	2	3	3	3	2	2	3	1	0	22	4	4	4	4	3	3	4	3	1	3	33
D	3	3	2	3	3	1	1	3	0	0	19	4	3	4	4	3	3	4	3	0	2	30
E	3	2	2	2	2	0	0	1	0	0	12	4	4	3	4	3	3	4	3	0	0	28
F	2	2	0	0	0	0	0	0	0	0	4	4	4	4	4	2	1	4	3	0	0	26
G	3	2	0	0	0	0	0	0	0	0	5	4	4	4	4	3	1	4	1	0	0	25
H	2	2	0	0	0	0	0	0	0	0	4	3	3	3	3	1	2	3	0	0	0	18
I	2	2	0	0	0	0	0	0	0	0	4	3	3	0	0	0	0	3	0	0	0	9
J	1	0	0	0	0	0	0	0	---	0	1	1	0	0	0	0	0	0	0	0	0	1
K	0	0	---	0	---	---	0	0	---	---	0	0	0	0	0	0	0	0	0	0	0	0
L	0	0	---	---	---	---	---	---	---	---	0	0	0	---	---	---	---	---	0	---	---	0
M	0	0	---	---	---	---	---	---	---	---	0	---	---	---	---	---	---	---	---	---	---	---
Total	---	---	---	---	---	---	---	---	---	---	191	---	---	---	---	---	---	---	---	---	---	453

Summary:

Number of spikelets from rusted plants producing—
- 4 kernels = 0
- 3 kernels = 24
- 2 kernels = 48
- 1 kernel = 23
- 0 kernel = 124

Summary:

Number of spikelets from check plants producing—
- 4 kernels = 42
- 3 kernels = 63
- 2 kernels = 36
- 1 kernel = 24
- 0 kernel = 66

[a] As shown in Table 2, 47 heads of each were studied; 10 were selected to illustrate the results obtained.
[b] Sequence of letters indicates approximate order of blossoming of spikelets from the central part of the head each way.

The results of a similar study of the heads of Michigan Amber grown in the greenhouse in rows are shown in Tables 2 and 4 and in Figure 4. The heads so produced were much shorter than when the plants were spaced in pots. As shown in Table 2 (1927, B), the rusted plants did not produce any spikelets having four kernels, while 22 such spikelets were produced by the check plants. In the rusted plants there also was a decided reduction in the number of spikelets producing three kernels. Table 4 shows the number of

kernels per spikelet in 13 heads from rusted and 13 from check plants. Here, again, the spikelets producing three and four kernels are abundant in the central portion of the heads of the check, while they are relatively infrequent in the rusted plants. Sterile spikelets are some-

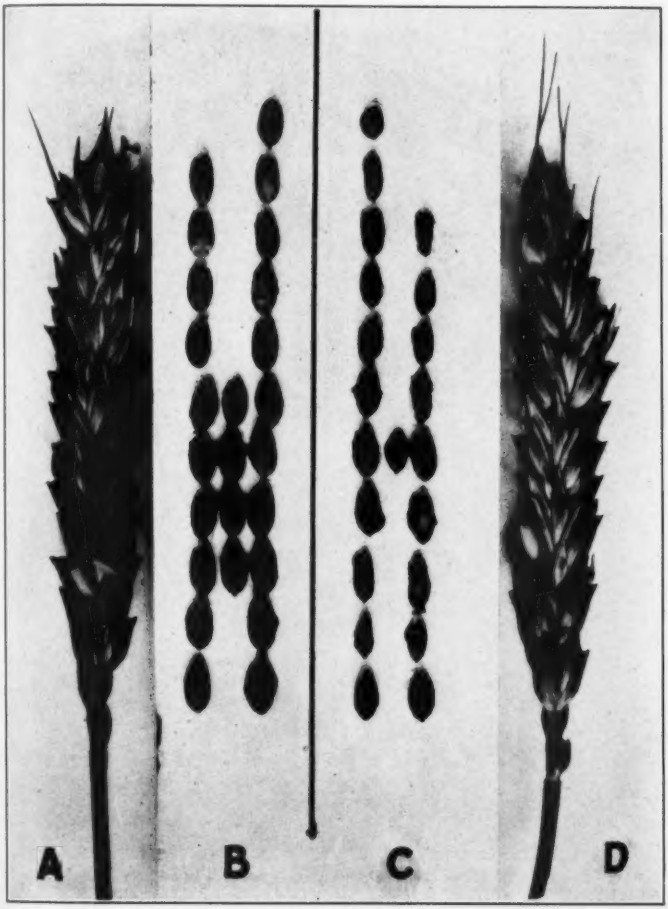

FIGURE 4.—Effect of leaf rust on the number of kernels per spikelet of Michigan Amber wheat in relation to their position on the head: A, Head from check plant (C); B, kernels of each spikelet from A arranged as they occurred in the spikelet; C, kernels of each spikelet from D arranged as they occurred in the spikelet; D, head from a rusted plant (R)

what more abundant in the upper and lower portions of the heads of the rusted plants.

In a similar way, the 150 heads from the dusted and the rusted (undusted) rows of Illinois No. 1 grown in the field in 1927 were studied. The results are given in Tables 2 and 5. As shown in Table 2, there were fewer spikelets producing three and four kernels in the rusted plants. In Table 5 and Figure 5 the kernels per spikelet are

shown as they occurred in 13 heads each of rusted and dusted plants. In both cases the spikelets containing three kernels were located in the central portion of the heads. About twice as many developed in the dusted as in the rusted plants. There was very little difference

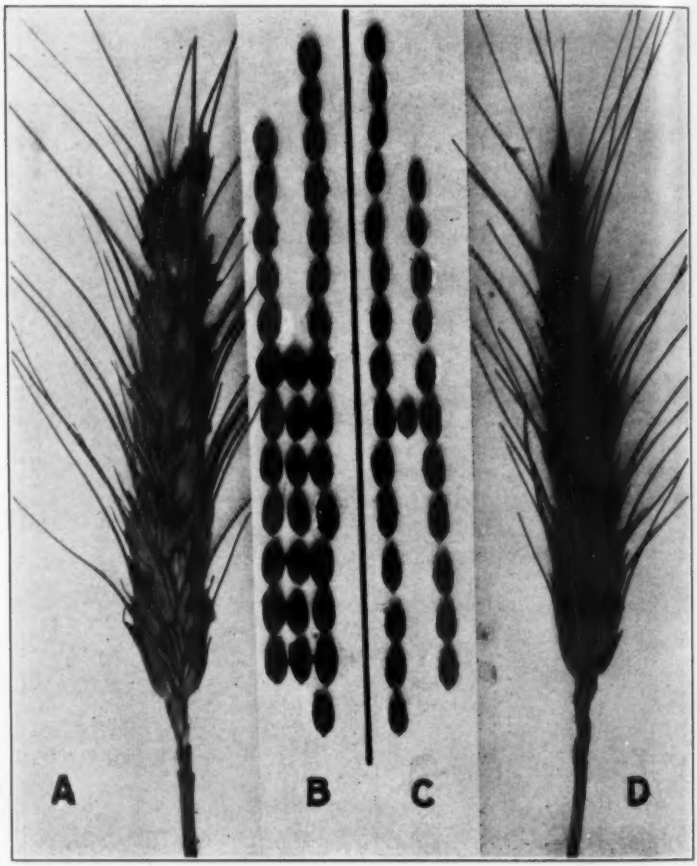

FIGURE 5.—Effect of leaf rust on the number of kernels per spikelet of Illinois No. 1 wheat in relation to their position on the head: A, Head from a plant in the sulphur-dusted plot (D); B, kernels of each spikelet from A arranged as they occurred in the spikelet; C, kernels of each spikelet from D arranged as they occurred in the spikelet; D, head from a heavily rusted plant (R)

in the number of sterile spikelets. The sample of the 13 heads reported in Table 5 would indicate a slight increase in number for the dusted heads. However, as shown in Table 2, the 150 heads from rusted plants had a few more sterile spikelets than the check heads.

TABLE 4.—*Number of kernels per spikelet in relation to position in heads of rusted and check plants of Michigan Amber wheat grown in rows in the greenhouse at La Fayette, Ind., in 1927* [a]

Arrangement of spikelets [b]	Heads from rusted plants: Number of kernels per spikelet in head—													Total kernels	Heads from check plants: Number of kernels per spikelet in head—													Total kernels
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10	No. 11	No. 12	No. 13		No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10	No. 11	No. 12	No. 13	
H'	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	2	0	0	0	1	1	1	1	0	1	9
G'	1	2	0	1	1	0	0	0	0	0	1	0	1	7	2	0	1	2	0	2	2	1	1	3	1	1	1	17
F'	1	1	1	2	2	1	1	1	0	1	1	0	1	13	2	1	1	2	1	2	2	2	2	1	2	2	1	21
E'	1	2	1	2	3	2	1	2	1	1	1	1	2	20	2	1	1	2	1	3	1	2	2	2	2	1	2	22
D'	2	2	1	2	2	2	2	2	0	2	0	2	2	21	2	2	2	2	2	2	2	3	2	2	2	1	2	26
C'	2	2	1	1	2	2	2	1	2	1	2	1	1	20	2	2	2	2	2	3	2	3	3	2	2	2	2	29
B'	2	3	2	2	2	2	2	2	1	2	2	3	1	26	2	2	2	1	2	3	3	3	3	2	2	2	2	29
A'	2	2	0	2	3	1	1	2	2	2	2	3	1	23	2	1	1	2	1	3	3	3	3	2	2	3	1	27
A	1	2	2	2	2	2	1	2	2	2	2	3	1	24	2	1	2	1	2	4	3	3	3	2	2	2	2	29
B	1	2	0	2	3	2	0	2	1	2	2	3	0	20	2	1	2	1	2	4	2	3	3	2	1	3	1	27
C	0	2	0	2	3	2	0	1	2	2	1	2	0	17	2	0	1	0	1	4	3	3	3	2	2	2	0	23
D	0	0	0	0	1	2	0	0	2	2	2	3	0	12	1	0	0	0	0	4	2	3	3	1	0	2	0	16
E	0	0	0	0	2	0	0	0	2	1	2	2	0	9	0	0	0	0	0	2	0	2	2	2	0	0	0	6
F	0	0	0	0	0	0	0	0	2	0	0	1	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	3
G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2
H	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total														216														287

Summary:

Number of spikelets from rusted plants producing—
- 4 kernels = 0
- 3 kernels = 10
- 2 kernels = 71
- 1 kernel = 44
- 0 kernel = 96

Summary:

Number of spikelets from check plants producing—
- 4 kernels = 4
- 3 kernels = 27
- 2 kernels = 76
- 1 kernel = 38
- 0 kernel = 76

[a] As shown in Table 2, 246 heads of rusted plants and 241 heads of the check plants were studied; 13 heads were selected to illustrate the results obtained.

[b] Sequence of letters indicates approximate order of blossoming of spikelets from the central part of the head each way.

This distribution of kernels is significant when the sequence of blossoming is taken into consideration. Blossoming usually starts in the central portion of the head. The outer flowers of the spikelets blossom first, followed by the inner flowers in their order on the rachilla. Blossoming progresses upward and downward from the central portion of the head. As the upper and lower spikelets, and the inner flowers of the central spikelets, more often fail to develop kernels in the heads of rusted plants than in those of the dusted plants, it is evident that infection prevents the development of kernels in the late-blooming flowers.

TABLE 5.—*Number of kernels per spikelet in relation to position in heads of rusted and sulphur-dusted plants of Illinois No. 1 wheat grown in the field nursery at La Fayette, Ind., 1927* [a]

Arrangement of spikelets [b]	Heads from rusted plants														Heads from check (dusted) plants													
	Number of kernels per spikelet in head—													Total kernels	Number of kernels per spikelet in head—													Total kernels
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10	No. 11	No. 12	No. 13		No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10	No. 11	No. 12	No. 13	
L'																					1							1
K'																												
J'	1	--	1											2	1	0	--				1	--						1
I'	1	--	1									1	--	3	1	1	1	1	1	1	0	1	--	1	0	--	--	1	8
H'	1	0	1	1	--	--	1	0	1	--	1	1	1	8	2	2	2	1	1	1	0	2	2	2	1	0	2	2	18
G'	2	1	2	1	1	1	1	1	1	1	2	1	1	16	2	2	2	2	1	2	1	1	2	1	1	1	2	2	20
F'	2	1	2	2	1	1	2	1	2	1	2	2	1	20	2	2	2	2	1	1	2	2	2	2	1	1	2	2	22
E'	2	1	2	2	2	1	2	1	2	2	2	2	1	22	2	2	2	2	2	2	2	2	2	2	1	3	2	26
D'	2	2	2	2	2	2	2	2	2	2	2	2	2	26	2	2	2	2	2	2	2	2	2	2	2	3	2	27
C'	2	2	2	2	2	2	2	2	2	2	2	2	2	26	2	2	2	1	2	2	2	3	2	2	2	3	2	27
B'	3	2	2	2	1	1	2	2	2	2	2	2	2	25	2	2	3	1	2	1	3	3	3	1	2	3	3	29
A'	3	2	2	2	1	3	3	2	2	2	3	2	2	29	3	3	3	3	3	3	3	3	3	2	2	3	3	37
A	3	2	2	2	1	3	2	2	2	2	3	2	2	28	3	3	3	3	3	3	3	3	3	2	2	3	3	37
B	3	2	2	3	1	1	3	2	3	2	2	2	2	28	3	3	3	2	3	2	3	3	3	2	2	3	3	35
C	3	2	2	2	1	2	3	2	3	2	3	2	2	29	3	3	3	2	2	2	2	2	3	2	2	3	3	32
D	3	2	2	2	1	3	3	2	3	0	3	2	0	26	3	3	3	2	2	2	3	2	3	2	2	3	3	33
E	3	1	2	2	0	2	2	1	3	0	3	2	2	23	3	3	3	2	2	1	3	2	2	2	0	3	3	29
F	1	0	2	2	0	0	2	2	0	2	0	2	1	16	3	3	1	1	2	0	3	2	2	2	0	3	2	24
G	0	0	0	0	0	0	2	2	0	0	0	0	0	7	2	2	0	0	1	0	3	1	2	0	0	2	0	13
H	0	0	0	0	0	--	--	0	0	0	--	2	0	2	0	2	0	0	0	0	2	0	1	0	0	1	0	6
I	0	--	0	--	--	--	--	--	--	0	--	0	0	0	0	0	0	0	0	0	1	--	0	0	--	--	0	1
J															0	0	--	--	--	0	0	--	0	--	--	--	0	0
K															0	--	--	--	--	--	0	--	--	--	--	--	--	0
L																					0	--	--	--	--	--	--	0
Total														336														428

Summary:

Number of spikelets from rusted plants producing	
	3 kernels= 25
	2 kernels=108
	1 kernel = 45
	0 kernel = 33

Summary:

Number of spikelets from check plants producing	
	3 kernels=65
	2 kernels=97
	1 kernel =39
	0 kernel =41

[a] As shown in Table 2, 150 heads of each were studied; 13 were selected to illustrate the results obtained.
[b] Sequence of letters indicates approximate order of blossoming of spikelets from the central part of the head each way.

EFFECT ON OVERWINTERING OF WHEAT

In the fall of 1922 a series of field sowings was made to obtain information on the effect of the development of leaf rust on wheat sown in the fall. Seed of the Trumbull variety was sown on three different dates, September 8, September 20, and October 3, in plots 17 by 50 feet. In each of these plots six areas, each 3 feet square, were covered with muslin cages. (Fig. 6, A.) Plants in three of these cages were inoculated with the leaf rust of wheat, and those in three others, alternating with the first three, were maintained free from rust.

In the first plot, sown September 8, inoculations were made on September 20. By October 4 a moderate infection had developed on the older leaves. The rust increased slowly during October, the new leaves becoming infected as they developed; a severe infection had developed by November 13. No rust developed in the check cages, and the wheat from them will be designated hereafter as rust free.

In the second plot, sown September 20, plants in three of the cages were inoculated on October 15. A slight amount of rust had appeared by October 31, and by November 13 a moderate infection had developed on the older leaves. No rust developed in the cages containing the check plants.

The third plot, sown October 3, was inoculated on October 25, and a slight scattered infection had developed by November 13. No rust occurred in the check cages. On November 21 all the cages were removed. Both the infected and rust-free wheat under the cages had

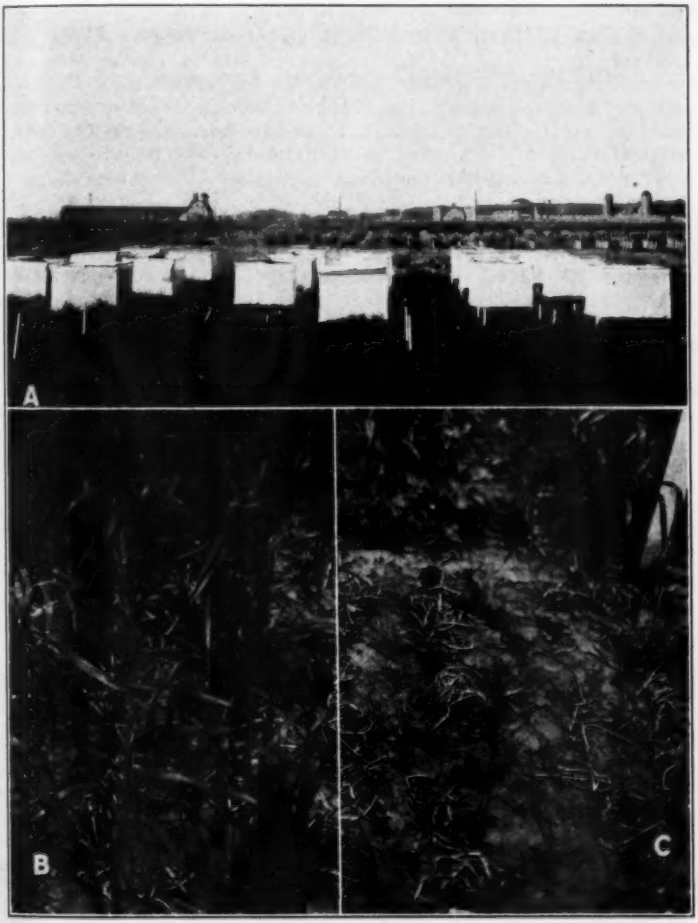

FIGURE 6.—Effect of leaf rust on winterkilling of wheat: A, Early fall sowing showing caged areas; B, spring survival in an area free from rust in the fall; C, spring survival in one of the areas severely rusted in the fall

made rank growth and therefore was not in good condition for overwintering.

On May 2, counts were made to determine the survival. The average stand in rusted areas of the first sowing was 4.1 per cent. (Fig. 6, C.) The average for the rust-free areas was 77.7 per cent. (Fig. 6, B.) In the second sowing the stand in the rusted areas was 17.6 per cent and in the rust free 77.7 per cent. In the third sowing the rusted areas had a stand of 48.6 per cent and the rust free 55.1 per cent.

In the case of the early sown and severely rusted wheat, the infection was responsible for a very pronounced increase in winterkilling. The second sowing was less severely rusted and the rusted areas showed less winterkilling, although almost four times as much as the check. The inoculated wheat of the late sowing was only slightly infected, and there was no very significant difference between the winterkilling of these rusted areas and the rust-free check areas. However, in the late sowing, there was a considerable increase of winterkilling in the rust-free plots over similar plots of the earlier sowings. Unquestionably, the effect produced by caging was responsible for a portion of the winterkilling. However, the results indicate that leaf rust, when present in abundance, may be a considerable factor in causing winterkilling.

DISCUSSION

The results of these investigations indicate that the effect of the leaf rust of wheat varies with the severity of infection and the stage of development of the wheat. Under the conditions of these experiments, a moderate infection occurring from early in the wheat development (tillering) to maturity resulted in 57.2 to 63.3 per cent reduction in yield. A severe infection occurring throughout the same period was responsible for a reduction of 97.4 per cent. A somewhat later severe infection reduced the yield 91.3 per cent. A severe infection developing just before the heads emerged from the boot resulted in a reduction of 54.3 per cent. Severe infections occurring from head emergence to maturity resulted in 37.2 per cent reduction. Severe infection from blossoming to maturity produced 24 to 33 per cent reduction. Moderate infection, following blossoming and increasing to a maximum before maturity, resulted in 11.1 per cent reduction.

Reduced yield results from production of fewer and also of lighter kernels by the rusted plants. In the case of infections occurring relatively early, a large proportion of the reduction in yield was due to fewer kernels, although the reduction in weight of the kernels is an important factor. In the case of late infections, the reduction in number of kernels is still an important factor, but the reduction in weight per kernel plays a proportionately greater part.

Although no critical study of the effect of leaf rust on the quality of the grain was made, there appears to be no very outstanding difference. Under conditions of severe infection over fairly long periods, rusted plants produced more shriveled kernels. Field observations indicate that under conditions of severe drought abundant leaf-rust infection may result in considerable shriveling. According to Weaver (*16*), H. B. Humphrey found that the leaf rust of wheat had a very pronounced effect upon transpiration, increasing it 38 per cent when the uredinia of the rust occupied less than 1 per cent of the transpiring surface. Under conditions of drought, leaf rust therefore may be of unusual importance.

In one experiment in 1927, leaf rust apparently caused an increase in the amount of yellow berry. As no differences in this respect were noted in other experiments, it is questionable how important the rust may be in that connection. It suggests that under conditions favoring the production of yellow berry the disturbance in metabolism produced by the rust sometimes may increase the proportion of such kernels. Usually, however, it would appear that leaf rust has no

pronounced effect upon the quality of grain, and this probably accounts in part for the earlier opinions that leaf rust was of little or no importance in wheat production.

Leaf rust reduces not only the yield of grain but also that of the straw. The severe infections occurring early prevented the development of many culms and caused a reduction of 70 per cent or more. Later infections reduced the weight of straw from 11 to 33 per cent. While no analyses of straw were attempted, the effect on color is suggestive. The Michigan Amber variety in 1927 developed purple color in the check plants when they were maturing, while the rusted ones were a dull yellow. This would indicate a shortage of carbohydrates in the rusted plants.

That the amount of functioning leaf area is important in determining the yield of wheat has been demonstrated by a number of investigators. Kiesselbach (*6*) studied the effect of removing leaves at different stages in plant development. When leaves were removed 3 days after heading (25 days before maturity) the yield of grain was reduced from 36.9 to 28.6 gm., or 22.5 per cent. The weight of straw was reduced from 4,284 to 3,603 gm., or 15.8 per cent. When the leaves were removed 10 days after heading (18 days before maturity) the weight of grain was 32.4 gm., a reduction of 12.2 per cent, and the weight of straw was 3,796 gm., a reduction of 11.3 per cent. When the leaves were removed 17 days after heading (11 days before maturity) the yield of grain was 35.4 gm., a reduction of 4.0 per cent, and the yield of straw was 4,050 gm., a reduction of 5.4 per cent. Roebuck and Brown (*14*) studied the effect on stripped (all the leaves removed), half-stripped (one-half of each leaf removed), and bottom-stripped (all the lower leaves removed) plants for periods of one, two, three, four, five, six, and seven weeks. Expressing their data in terms of percentage reduction in grain produced, the yield of plants of both varieties completely stripped for a period of seven weeks was reduced 42.9 per cent, for four weeks 24.9 per cent, and for one week 5.5 per cent. The yield of plants with half of each leaf removed for seven weeks was reduced 48.9 per cent, for four weeks 19.0 per cent, and for one week 10.6 per cent. The yield of plants with all the lower leaves removed for seven weeks was reduced 41.4 per cent, for four weeks 18.8 per cent, and for one week 4.8 per cent. Leaf rust not only reduces the leaf area of the wheat plant but also modifies the metabolism of its host. According to Weaver (*16*), it also increases its rate of transpiration. Other functions probably also are seriously affected, for Reed and Cooley (*13*) have shown that in apple leaves infected with *Gymnosporangium juniperi-virginianae* the average rate of assimilation of carbon dioxide was only about one-half that in the healthy plants.

That severe infection of a highly resistant variety may cause a decided decrease in yield is shown by the results obtained with the Webster variety. As has been stated, physiologic form 5 causes a rapid necrosis resulting in a production of small flecks and the death of the rust. When plenty of inoculum is present and abundant infections occur, the leaves of such infected plants die earlier than do those of check plants. The resulting reduction in functional leaf area therefore should bring about a reduction in yield. The 11.4 per cent reduction in yield noted for Webster is well within the expectation for the reduction of functioning leaf area. In nurseries where

varieties are being compared in rows, resistant varieties usually are subject to severe infection from neighboring susceptible varieties and the yield probably is reduced. However, where such resistant varieties are sown in large areas, especially in the absence of susceptible varieties, such an effect is not to be expected. Infection from distant susceptible varieties will be slight, and if the rust is unable to develop spores on the resistant variety it can not multiply and spread. Tests of resistant varieties in close comparison with susceptible varieties probably do not indicate the full yielding ability of the resistant varieties when sown in large areas.

A study of the effect of the rust upon kernel production in comparison with blossoming indicates that there is a fairly close correlation with time of blossoming. The first flowers to open are the outer ones of the central spikelets. Blossoming then progresses up and down in the spike and inward in the spikelets. In rusted plants the grain is produced only by the earlier flowers—the outer of the central spikelets and a portion of the upper and lower spikelets. The check plants develop grain also in the inner flowers of the central spikelets and in more of the outer flowers of the upper and lower spikelets. With increased severity of the rust the kernel production is more closely restricted to the earliest flowers. This indicates that the rust is responsible for a reduction in the materials necessary for kernel development. Under such conditions the first flowers to be pollinated obtain the available material and develop, while the later flowers are unable to develop because of lack of available material. Even in the early flowers the shortage of material results in somewhat smaller and lighter kernels. The effect of very late infection, after kernel development of the head in general is in a fairly advanced stage, is largely a reduction in weight of kernels, especially in the late flowers.

Severe autumnal infection of winter wheat may be an important factor favoring winterkilling, as has been shown by the marked increase in winterkilling where early sown wheat was heavily rusted. Infection on fall-sown grain takes place from volunteer wheat, and the spread from such sources usually is slow. Over a considerable portion of the soft-winter-wheat belt wheat is sown late, usually about October 1 in the vicinity of La Fayette, Ind., in order to escape infestation with the Hessian fly. Where such is the practice, the natural infection from volunteer wheat usually is rather slight. With earlier sowings the chances for development of the rust increase, and when conditions are favorable for infection and spread leaf rust may be an important factor affecting winter survival.

The leaf rust of wheat is more or less prevalent throughout the wheat-growing areas of the United States. It is especially prevalent and severe in the soft-winter-wheat area. Since 1917 the Plant Disease Survey of the Bureau of Plant Industry, United States Department of Agriculture, has been collecting information from collaborators in various States concerning the prevalence and severity of plant diseases. A review of this information shows that in the soft-winter-wheat area, at least, leaf rust has been present to some extent each year. In 1918, as summarized by Haskell,[8] leaf rust was particularly

[8] HASKELL, R. J. Op. cit. (See footnote 4.)

severe in the eastern and southeastern United States. The estimated average percentages of total leaf area affected, as determined by a survey throughout the eastern wheat area, are shown in Table 6. It is interesting to note that for 1918 no collaborator of the Plant Disease Survey [9] estimated the reduction in yield due to leaf rust as more than a trace.

TABLE 6.—*Estimated average percentages of total leaf area of wheat affected by leaf rust in 1918 in the States named*

[U.=unreported because loss was insignificant; T.=trace]

Section and State	Leaf area affected	Section and State	Leaf area affected
New England:	*Per cent*	South-Central, East—Continued.	*Per cent*
Maine	15.0	Georgia	26.3
New Hampshire	12.0	Alabama	30.5
Vermont	19.0	Mississippi	25.9
Massachusetts	7.6	Kentucky	30.3
Connecticut	9.2	Tennessee	28.0
North-Central, East:		North-Central, West:	
New York	17.0	Minnesota	7.0
Pennsylvania	48.7	Iowa	13.0
Delaware	U.	North Dakota	U.
New Jersey	43.0	South Dakota	9.6
Maryland	28.9	Nebraska	5.0
West Virginia	47.9	Colorado	T.
Ohio	28.8	Montana	T.
Indiana	U.	Wyoming	T.
Michigan	20.6	South-Central, West:	
Wisconsin	39.7	Missouri	8.3
Illinois	6.5	Kansas	5.2
South-Central, East:		Arkansas	U.
Virginia	37.9	Oklahoma	6.6
North Carolina	29.7	Louisiana	55.8
South Carolina	35.8	Texas	1.4

In 1919 the leaf rust of wheat was unusually severe. Johnson and Haskell,[10] in their summary of cereal diseases for that year, stated that some fields in Georgia and Arkansas were so severely infected that they were abandoned in the spring of 1919. In the southeastern United States the winter was mild and the rust developed late into the winter and resumed growth early in the spring, resulting in early severe infections. Northward the rust was less severe, although wheat was heavily rusted. In the Western and Northwestern States the rust was relatively slight except locally in certain irrigated sections. Estimates of the leaf surface infected are not given. However, the rust was of such severity that a definite loss was estimated for the various States in the eastern half of the country varying from 0.5 to 8 per cent reduction in yield. The estimated reduction in yield due to leaf rust, as summarized by the Plant Disease Survey,[11] is shown in Table 7. On this basis the loss from leaf rust for the United States in 1919 was 1.47 per cent, or 16,633,000 bushels.

[9] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. CROP LOSSES FROM PLANT DISEASES—1918. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bul. Sup. 6: 186–213. 1919. [Mimeographed.]

[10] JOHNSON, A. G., and HASKELL, R. J. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1919. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bul. Sup. 8: 1–81, illus. 1920. [Mimeographed.]

[11] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1919. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bul. Sup. 12: 307–332. 1920. [Mimeographed.]

TABLE 7.—*Estimated percentage annual and 9-year average reduction in wheat yield in the 9 years from 1919 to 1927, inclusive, in the States named*

[U. = unreported because loss was insignificant; T. = trace]

Section and State	Estimated percentage reduction in yield									
	1919	1920	1921	1922	1923	1924	1925	1926	1927	9-year average
New England:										
Maine	U.	U.	U.	U.	U.	U.	U.	U.	U.	U.
New Hampshire	U.	U.	U.	U.	U.	U.	U.	U.	U.	U.
Vermont	0.5	T.	0	U.	1	0.5	U.	U.	U.	0.2
Massachusetts	U.	U.	0	T.	U.	U.	U.	U.	U.	0
Connecticut	.5	U.	U.	T.	U.	U.	0.25	U.	U.	.08
Rhode Island	U.	U.	U.	U.	U.	U.	U.	U.	U.	U.
North-Central, East:										
New York	1	T.	3	3	1	1	1.5	1	1	1.4
Pennsylvnia	1	T.	2	4	1.5	1	.3	.5	6	1.8
Delaware	2	.2	3	2	.2	.1	U.	T.	T.	.8
New Jersey	1	T.	10	U.	.2	T.	T.	.5	U.	1.3
Maryland	2	1.5	6	.5	1.5	2	1	.5	.5	2.2
West Virginia	3	T.	5	18	1	T.	T.	T.	1	3
Ohio	1	T.	4	5	4	U.	.1	T.	.5	1.6
Indiana	1	.1	7	10	2	T.	T.	5	13	4.2
Michigan	1	T.	U.	2	T.	.5	0	2	1	.7
Wisconsin	1	T.	T.	1	T.	1	1	1	T.	.6
Illinois	1	.5	1	10	3	2.4	1.5	1	2.5	2.5
South-Central, East:										
Virginia	3	2	5	5	1	1	T.	T.	1.5	2.1
North Carolina	5	3	20	U.	3	3	5	T.	3	4.7
South Carolina	5	2	2	10	2	1	2	1	2	3.0
Georgia	8	2	3	5	5	5	3	U.	U.	3.4
Alabama	5	2	U.	3	5	U.	U.	U.	U.	1.7
Mississippi	5	4	3	2	1	0	U.	U.	U.	1.7
Kentucky	2	1	U.	10	1	T.	.1	T.	U.	1.6
Tennessee	4	T.	10	15	2	U.	1	T.	20	5.8
North-Central, West:										
Minnesota	1	T.	T.	.5	T.	T.	T.	T.	3	.5
Iowa	1.5	1	T.	T.	1.5	T.	5	6	15	3.3
North Dakota	1	1.5	3	1	1	T.	T.	T.	2	1.1
South Dakota	.5	1	5	T.	1	0	0	T.	3	1.2
Nebraska	1.5	1	U.	U.	1	T.	T.	T.	2	.6
Montana	0	0	1	T.	U.	T.	0	0	T.	.1
Wyoming	U.	U.	U.	T.	U.	0	0	U.	U.	0
Colorado	.1	T.	U.	T.	1	0	0	0	T.	.1
South-Central, West:										
Missouri	2	1	U.	U.	1	U.	U.	0	T.	.4
Kansas	1.5	T.	1	1	1	T.	0	T.	8	1.4
Arkansas	8	2	5	5	4	T.	T.	T.	U.	2.7
Oklahoma	4	2	5	5	U.	0	U.	U.	U.	1.8
Louisiana	U.	T.	U.	U.	U.	T.	T.	U.	U.	0
Texas	4	1	T.	1	1	1	.5	1	3	1.4
New Mexico	U.	T.	U.	U.	U.	U.	U.	U.	T.	0
West:										
Idaho	0	T.	0.5	0	T.	0	T.	T.	T.	.06
Utah	U.	T.	.2	T.	.3	.1	.5	U.	T.	.1
Arizona	U.	T.	U.	U.	U.	U.	U.	.5	U.	.06
Washington	0	T.	T.	0	T.	T.	0	T.	T.	0
Oregon	0	T.	T.	T.	T.	T.	T.	.5	T.	.06
California	T.	T.	2	T.	T.	0	1	U.	U.	.3
Nevada	T.	T.	U.	0	U.	U.	U.	U.	U.	0

Fromme,[12] in his summary of cereal diseases for 1920 for the Plant Disease Survey, stated that leaf rust in general was less severe than in 1919. It was most prevalent and destructive in the Southern States, less prevalent in a belt from Pennsylvania westward to Kansas and Iowa, and more prevalent in North Dakota, Minnesota, and upper Michigan. The estimate of losses in yield for 1920 as given by the Plant Disease Survey [13] is shown in Table 7. The estimated total reduction for the United States is given as 0.6 per cent, or 5,318,000 bushels.

[12] FROMME, F. D. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1920. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bul. Sup. 15: 115–176, illus. 1921. [Mimeographed.]

[13] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1920. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bul. Sup. 18: 317–338. 1921. [Mimeographed.]

Stakman,[14] in his summary of cereal diseases for 1921 for the Plant Disease Survey, reported that leaf rust probably was more prevalent than it had been for several years. The rust was abundant on wheat in the fall of 1920, and in the South it developed to some extent throughout the winter. Various observers noted that it developed early in the spring. This resulted in an early, severe infection in which not only the leaves but in some cases the glumes also were severely rusted, resulting in premature ripening. In West Virginia and Oklahoma drought was considered to have increased the resultant damage. The rust was much more prevalent on the Pacific coast than in the previous two years, causing damage especially in the valleys. As pointed out by Stakman, the rust was most prevalent and severe in the soft-winter-wheat area. The estimated reduction in yield for 1921 as given by the Plant Disease Survey[15] is shown in Table 7. The estimated reduction for the United States is given as 1.9 per cent, or 16,944,000 bushels.

Haskell and Wood,[16] in their summary of cereal diseases for 1922 for the Plant Disease Survey, show that the leaf rust of wheat was again very severe throughout the soft-winter-wheat area. It apparently was more generally destructive than in any previous year. The rust was rated as the most important disease of wheat in 1922 by those reporting from New York, Delaware, Maryland, Virginia, West Virginia, South Carolina, Indiana, Illinois, Tennessee, Mississippi, Oklahoma, and Arkansas, and as the disease second in importance by those in Pennsylvania, Georgia, Ohio, Wisconsin, and North Dakota. In Georgia the rust was severe early in the plant development, when the wheat was about 1 foot high. The leaves were prematurely killed, and farmers were so alarmed that they inquired concerning the advisability of cutting their wheat for hay, pasturing it, or plowing it under. At Experiment, Ga., Prof. R. P. Bledsoe estimated the loss as likely to reach 50 per cent, stating that wheat was yielding 14 bushels there as compared with 30 bushels in the year before. In Virginia, Tennessee, and Kentucky, leaf rust started somewhat later in the spring but reached a severity comparable with that of the previous season. In southern Indiana it was one of the principal factors contributing toward low yields, it being estimated as bringing about a 20 per cent reduction. Tehon (*15*) placed the destruction of leaf area in Illinois at 50.3 per cent.

The Plant Disease Survey [17] gave the estimates of reduction in yield for 1922, as shown in Table 7. The reduction in yield for the entire United States for 1922 is given as 2.5 per cent, or 23,107,000 bushels.

Leaf rust was less destructive in 1923 than in the two previous seasons.[18] The winter of 1922–23 was unfavorable for the overwintering of the rust, and the cool spring and early summer held it in check. Consequently, the rust was slow in developing and reached a maxi-

[14] STAKMAN, E. C. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1921. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bul. Sup. 21: 139–254, illus. [Mimeographed.]

[15] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1921. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bul. Sup. 24: 489–510. 1922. [Mimeographed.]

[16] HASKELL, R. J., and WOOD, J. I. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1922. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Bul. 27: 164–266, illus. 1923. [Mimeographed.]

[17] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1922. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr Sup. 30: 462–490. 1923. [Mimeographed.]

[18] HASKELL, R. J. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1923. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Sup. 35: 244–317, illus. 1924. [Mimeographed.]

mum only a short time before harvest. The reduction in yield for 1923, as given by the Plant Disease Survey,[19] is shown in Table 7. The reduction in yield in 1923 for the entire United States is given as 1.09 per cent, or 9,735,000 bushels.

In general there was much less leaf rust in 1924 than in 1923.[20] Many observers commented on the slight development. In Georgia it was very late, reaching only a moderate infection before harvest. In Tennessee it was the least that had been noted for a number of years. In Indiana it was considered the least in 6 years and in Kansas the least in 10 years. Tehon (*15*) gave the leaf area infected in Illinois as 19.1 per cent, compared with 31.3 per cent in 1923 and 50.3 per cent in 1922. Various factors contributed to this condition. An open winter with alternate freezing and thawing, and consequent destruction of the infected leaves of winter wheat, greatly reduced the overwintering of the rust. The generally cool spring retarded its development. The estimated reduetion in yield in 1924 for the United States, according to the Plant Disease Survey,[21] is shown in Table 7. The total estimated reduction for the United States is given as 0.23 per cent, or 2,213,000 bushels.

In 1925 leaf rust was less severe than in 1924.[22] The overwintering of the rust was reduced in many places by low temperatures and insufficient protection. The months of April, May, and June were unusually dry in the eastern part of the country, and rust development was greatly retarded. Tehon (*15*) gave the leaf area infected in Illinois as 17.1 per cent, compared with 19.1 per cent in 1924. In New York, Kightlinger and Whetzel (*8*) reported increasing the yield of winter wheat 18.5 per cent by reducing leaf-rust infection 48.2 per cent by dusting with sulphur. The reduction in yield for 1925, as estimated by the Plant Disease Survey,[23] is shown in Table 7. The total reduction for the United States is given as 0.2 per cent, or 1,814,000 bushels.

The leaf rust of wheat was slightly more prevalent and destructive in 1926 than in 1925.[24] It by no means approached its prevalence during the period from 1918 to 1923, inclusive. In the southeastern United States an unusually dry spring prevented rust development to such an extent that only a trace occurred throughout much of the region, moderate infection developing very late locally, especially in low areas. Northern Texas and southern Oklahoma had heavy infections. Northern Oklahoma and southern Kansas had a moderate amount of rust early in the season, but dry weather prevented much further increase. There was a slight overwintering of leaf rust in Indiana, but development was retarded by cool weather. A moderate to heavy infection developed late. A similar situation occurred in

[19] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1923. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Sup. 36: 318–348. 1924. [Mimeographed.]

[20] MELCHERS, L. E. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1924. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Sup. 40: 106–191, illus. 1925. [Mimeographed.]

[21] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1924. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Sup. 43: 381–410. 1925. [Mimeographed.]

[22] HASKELL, R. J. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1925. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Sup. 48: 301–381, illus. 1926. [Mimeographed.]

[23] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1925. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Sup. 49: 382–412. 1926. [Mimeographed.]

[24] KIRBY, R. S., and ARCHER, W. A. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1926. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Sup. 53: 110–208, illus. 1927. [Mimeographed.]

Wisconsin. The reduction in yield for 1926 for the United States, as estimated by the Plant Disease Survey,[25] is shown in Table 7. The total reduction for the United States is given as 0.4 per cent, or 3,990,000 bushels.

Leaf rust was considerably more prevalent and destructive in 1927 [26] than in previous years. There apparently was considerable overwintering, especially in the southern part of the country. From Pennsylvania was reported one of the most severe epidemics ever occurring in that State, with an average infection of 62 per cent. Low temperatures apparently held the rust somewhat in check throughout Indiana and Missouri, but a maximum development was reached before maturity. As shown in this paper, 11.1 per cent reduction in yield of winter wheat occurred in plots at La Fayette, Ind. The loss for the State probably averaged about 13 per cent. From Wisconsin was reported heavy leaf-rust infection in the milk stage of wheat development. The overwintering of rust throughout Texas, Oklahoma, and Kansas resulted in heavy infections early in the season. Reductions in yield of 2 to 20 per cent were reported from Kansas. In Iowa infections were very severe. ("Some fields were so severely infected early in the season that heads never formed, in others the plants were so badly checked in their growth that heads did not fill properly."—Archer.)[27] Infections of 80 to 100 per cent were common.

In the spring-wheat area, leaf rust was more prevalent and destructive than at any time during the period from 1918 to 1926, inclusive. It was reported as very severe on spring wheat in North Dakota. Plants were practically defoliated and heads ripened early in Minnesota. Stakman, according to Haskell,[28] estimated reductions in yield of susceptible varieties in Minnesota as 5 to 7 bushels per acre, based on results of sulphur-dusting experiments. The estimated reductions in yield for 1927 [29] are given in Table 7. The reduction in yield for the United States in 1927, due to leaf rust, is given as 29 per cent, or 28,626,000 bushels.

The States, arranged in descending order of the average reduction in yield due to leaf rust in the period from 1919 to 1927, inclusive, are: Tennessee, 5.8 per cent; North Carolina, 4.7 per cent; Indiana, 4.2 per cent; Georgia, 3.4 per cent; Iowa, 3.3 per cent; West Virginia, 3.1 per cent; South Carolina, 3.0 per cent; Arkansas, 2.7 per cent; Illinois, 2.5 per cent; Maryland, 2.2 per cent; Virginia, 2.1 per cent; Oklahoma, 1.8 per cent; Pennsylvania, 1.8 per cent; Alabama, 1.7 per cent; Mississippi, 1.7 per cent; Kentucky, 1.6 per cent; Ohio, 1.6 per cent; New York, 1.4 per cent; Kansas, 1.4 per cent; Texas, 1.4 per cent; New Jersey, 1.3 per cent; South Dakota, 1.2 per cent; North Dakota, 1.1 per cent; Delaware, 0.8 per cent; Michigan, 0.7 per cent; Wisconsin, 0.6 per cent; Nebraska, 0.6 per cent; Minnesota, 0.5 per cent; Missouri, 0.4 per cent; California, 0.3 per cent; Vermont, 0.2 per cent; Colorado, 0.1 per cent; Montana, 0.1 per cent; Utah, 0.1 per cent; Connecticut, 0.08 per cent; Idaho, 0.06 per

[25] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1926. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Sup. 56: 394-423. 1927. [Mimeographed.]

[26] HASKELL, R. J. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1927. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Sup. 62: 302-353. 1928. [Mimeographed.]

[27] HASKELL, R. J. Op. cit. (p. 314).

[28] HASKELL, R. J. Op. cit. (See footnote 22.)

[29] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1927. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. Sup. 64: 370-399. 1928. [Mimeographed.]

cent; Arizona, 0.06 per cent; Oregon, 0.06 per cent; and Louisiana, Maine, Massachusetts, Nevada, New Hampshire, New Mexico, Rhode Island, Washington, and Wyoming, no loss large enough to be estimated. This shows that the rust was most severe in the soft-winter-wheat area, especially in the eastern and southeastern portions.

The losses due to the rust in some of the hard-winter-wheat and spring-wheat States are much greater than the percentage reduction would indicate, due to large acreages in such States as Kansas, Oklahoma, North Dakota, and South Dakota, as compared with the small acreages of such Southern States as Georgia, South Carolina, Alabama, and Mississippi, where the rust is much more severe. The total estimated reduction in yield in bushels for the 9-year period from 1919 to 1927, inclusive, by States, is shown in Table 8. The estimated total loss for the United States in the nine years is 108,380,000 bushels, or an average loss of 12,042,000 bushels per year.

Judging from the results obtained in these studies, the estimates of losses as determined by the collaborators for the Plant Disease Survey have been conservative. The leaf rust of wheat is more or less prevalent each year from the Rocky Mountains eastward. It is most prevalent and severe in the soft-winter-wheat States, and virtually every year it is a factor of importance in the production of soft winter wheat. While in both the hard-winter-wheat and spring-wheat States the rust is not so prevalent, the loss is important on account of the large acreage involved. When the rust is severe, as in 1926 in the hard-winter-wheat and in 1927 in the spring-wheat areas, it is a very important factor in wheat production in these areas.

TABLE 8.—*Estimated total reduction in wheat production, by States, caused by leaf rust, in the 9-year period from 1919 to 1927, inclusive*

[U.=unreported because the loss was insignificant]

Section and State	Reduction in production (bushels)	Section and State	Reduction in production (bushels)
New England:		North-Central, West:	
Maine	U.	Minnesota	1,660,000
New Hampshire	U.	Iowa	3,345,000
Vermont	2,000	North Dakota	10,280,000
Massachusetts	U.	South Dakota	4,213,000
Connecticut	U.	Nebraska	3,717,000
Rhode Island	U.	Montana	316,000
North-Central, East:		Wyoming	U.
New York	1,057,000	Colorado	221,000
Pennsylvania	4,388,000	South-Central, West:	
Delaware	125,000	Missouri	2,087,000
New Jersey	208,000	Kansas	16,413,000
Maryland	2,119,000	Arkansas	472,000
West Virginia	1,155,000	Oklahoma	7,726,000
Ohio	6,862,000	Louisiana	U.
Indiana	13,207,000	Texas	3,046,000
Michigan	1,261,000	New Mexico	U.
Wisconsin	208,000	West:	
Illinois	13,497,000	Idaho	147,000
South-Central, East:		Utah	127,000
Virginia	2,085,000	Arizona	6,000
North Carolina	2,700,000	Washington	U.
South Carolina	412,000	Oregon	101,000
Georgia	607,000	California	332,000
Alabama	98,000	Nevada	U.
Mississippi	35,000		
Kentucky	1,330,000		
Tennessee	2,815,000		

SUMMARY

Plants of the Mediterranean and Red Fern wheat varieties moderately infected with leaf rust from tillering to maturity had their yields reduced 63.3 and 57.2 per cent, respectively.

The yield of the Fulcaster variety, heavily infected from tillering to maturity, was reduced 97.4 per cent. Severe infection from shooting to maturity resulted in 91.3 per cent reduction. The yield of plants heavily rusted when the heads were just showing in the boot was reduced 54.3 per cent. The yield of plants heavily rusted in the period from blossoming to maturity was reduced 24.7 per cent.

The yield of Michigan Amber, heavily rusted when heads were emerging from the boot, was reduced 37.2 per cent. When 100 per cent infection was produced at blossoming, the yield was reduced 27.2 per cent in one case and 33.5 per cent in another.

By dusting with sulphur, leaf rust was greatly reduced in field plots. Undusted plots of the winter wheat Trumbull which became rusted from 50 to 100 per cent following blossoming yielded 11.1 per cent less than dusted plots. Undusted plots of the spring wheat Illinois No. 1 which became rusted 50 per cent at blossoming, increasing to 100 per cent later, yielded 24.2 per cent less than the dusted plots.

The leaves of rusted plants died in advance of the corresponding leaves on check plants, and the weight of the straw was decreased. In early infections the reduction was 70 per cent or more. Later infections reduced the weight of straw from 11 to 33 per cent, depending on the duration of the infection. In the case of the Michigan Amber variety, rust infection prevented purpling of the straw, suggesting a shortage of carbohydrates.

The yield of plants of the Webster variety, highly resistant to physiologic form 5, was reduced 11.4 per cent when they were abundantly infected during emergence of the heads from the boot. Although highly resistant, the leaves of infected plants died in advance of those of the checks. The reduction in yield was mostly due to slightly smaller and lighter kernels. Tests of resistant varieties adjacent to susceptible varieties probably do not indicate the entire yielding capacity possible when planted in large acreage.

Yield is reduced by the production of fewer and lighter kernels. Severe infections over long periods bring about a marked reduction in the number of kernels and also a decrease in the weight of kernels, whereas infections over shorter periods result largely in a decreased weight of kernels. Early infections increase the number of shriveled kernels. In late infections the kernels are slightly smaller and of less weight.

The reduction in number of kernels is correlated with relative time of blossoming. The late flowers, the flowers of the upper and lower spikelets, and the upper flowers of the central spikelets fail to develop kernels in the rusted plants to the same extent as in check plants.

Early, severe autumn infection may considerably increase the winterkilling of winter wheat.

Leaf rust usually is prevalent in the soft-winter-wheat area of the United States, and in most years it is an important factor in production. In the hard-winter-wheat and in the spring-wheat areas it frequently is not so severe as in the soft-winter-wheat area. In some years, as in 1926 in the hard-winter-wheat area and in 1927 in the spring-wheat area, it is a very important factor in wheat production.

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LEAF SPOT AND FOOT ROT OF KENTUCKY BLUEGRASS CAUSED BY HELMINTHOSPORIUM VAGANS [1] [2]

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INTRODUCTION

In an abstract [3] published in 1922 the writer reported the widespread occurrence on Kentucky bluegrass (*Poa pratensis* L.) of a leaf spot caused by a species of Helminthosporium. Often, especially in moist situations, the lesions had been found on the leaf sheaths at the base of the plants as well as on the blades, giving rise to a condition comparable to foot rot of wheat. A brief account of the parasite, containing a discussion of its distribution and its pathological effects in addition to its description under the name *Helminthosporium vagans* Drechs., was included the following year in a paper [4] dealing with various forms parasitic on grasses. Except for a report by Gardner [5] stating that leaf spot of June grass due to *H. vagans* was prevalent at La Fayette, Ind., during May, 1923, the literature seems to offer no information concerning the disease in which the parasite involved was referred to by the binomial mentioned. However, Monteith [6] reported that the leaf-spot disease of bluegrass had been destructive in fairways of golf courses in New Jersey and Pennsylvania during the early part of June, 1924. Although in the text the causal fungus was not cited by name, its identity was indicated in the statement that it was "closely related to those causing stripe, net blotch, spot blotch, and similar serious diseases of various grain crops." In a second paper [7] by the same writer extensive browning of bluegrass caused by the same leaf spot was noted as having occurred during May of the following year on some golf courses in the vicinity of Washington, D. C., and on the plots at the Arlington Experiment Farm, Rosslyn, Va. While the illustrations of severely affected leaves accompanying the text of the latter account appear altogether characteristic of those attributable to *H. vagans*, it may not be amiss to add that specimens of the diseased grass that formed the basis of Monteith's two reports had been submitted to the present writer for examination and the cause of the trouble had been determined as the parasite under consideration by microscopic inspection of the conidiophores and conidia present on the better developed lesions.

At the time the description of *Helminthosporium vagans* was drawn up [8] the writer's observations were limited to the development of the fungus on Kentucky bluegrass growing in fields or in lawns cut only

[1] Received for publication Oct. 12, 1929; issued March, 1930.

[2] A popular summary of this paper appeared in the following publication: DRECHSLER, C. LEAF SPOT AND FOOT ROT OF BLUEGRASS. Bul. Green Sect. U. S. Golf Assoc. 9: 120–123, illus. 1929.

[3] DRECHSLER, C. A NEW LEAF SPOT OF KENTUCKY BLUEGRASS CAUSED BY AN UNDESCRIBED SPECIES OF HELMINTHOSPORIUM. (Abstract.) Phytopathology 12: 35. 1922.

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[7] MONTEITH, J., JR. LEAF SPOT OF BLUEGRASS. Bul. Green Sect. U. S. Golf Assoc. 5: 198–199, illus. 1925.

[8] DRECHSLER, C. Op. cit., p. 687. (See footnote 4.)

at moderate intervals and then not excessively close. Although some material collected in Brooklyn, N. Y., in August, 1920, showed leaves that had withered as a consequence of infection, no instances of the killing of plants down to the ground had come to light. While, therefore, it was apparent that "under certain conditions of moisture and of temperature such as would favor a multiplication of foliar lesions and accentuate the foot-rot symptoms the damage may not be altogether unappreciable," the sparse scattering of lesions ordinarily displayed was held to mark the parasite as one of minor destructiveness. Later observations made, especially in fairways of golf courses, where more rigorous cutting is practiced, dictate a modification of this view. As the outward expression of the disease and its relation to the causal fungus still seem far from being generally recognized even among students dealing with troubles affecting the grasses, it may not be inappropriate to amplify the somewhat inadequate account previously submitted.

EFFECT OF THE PARASITE ON THE HOST

LEAF SPOT

In the earlier paper the foliar lesions were described as being of the spot-blotch type, appearing as areas of bluish-black coloration, diminishing in intensity about the margin. Such lesions are indeed found in all representative lots of material, but where conditions have been favorable for the development of the trouble they are outnumbered by morbid regions mostly of larger dimensions. The central areas of these regions are bleached to a straw color, leaving the bluish-black or dark-brown discoloration restricted to a marginal zone of varying width. As the lesions of the latter category, which manifestly conform to the eyespot type, bear conidiophores and conidia in the central bleached parts, the presumption follows that they represent the more advanced stages in the development of the spot-blotch lesions. The correctness of this presumption was proved when cultures obviously belonging to the same identical fungus were obtained on agar plates planted with excised spot-blotch lesions, with excised peripheral portions of eyespot lesions, and with bits of agar media from dilution plates each containing a single conidium from an eyespot lesion after germination. Indeed, the obvious transition of one type of lesion into another, exhibited in a collection of leaves like that shown in Figure 1, A–M, provided visible evidence scarcely less conclusive than the more formal proof by comparison of fungus cultures isolated from them.

A feature frequently noticeable in leaves of *Poa pratensis* affected with leaf spot is a symmetrical development or symmetrical pairing of lesions relative to the midrib. Manifestly, such arrangement is traceable to infection at an early stage in the growth of the leaf while the latter is still tightly folded, the fungus mycelium then permeating the double thickness of folded blade regardless of anatomical relationships. With the unfolding of the leaf the infected mass is naturally separated into corresponding halves. The symmetrical or paired disposition was thus more frequent than usual following the early severe outbreak of the disease in April, 1929, as is evident in Figure 1, which represents leaves collected in the District of Columbia, April 30, from a stand that had been allowed to grow up unmolested and was heading out at the time.

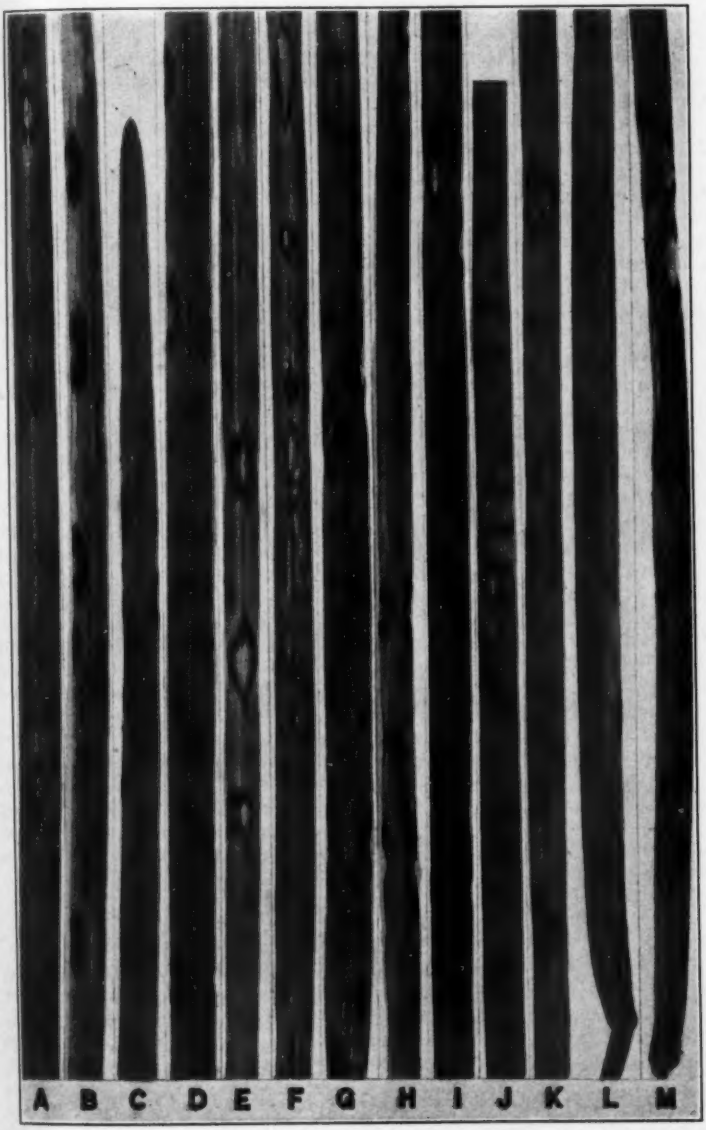

FIGURE 1.—A–M, Leaves of *Poa pratensis* affected with leaf-spot lesions due to *Helminthosporium sagans*. Collected April 30, 1929, in the District of Columbia, in a stand that had not been subjected to cutting. × 2

FOOT ROT

Even in bluegrass plants left to grow to full size, leaf-spot lesions occur at the bases as well as in other parts of the leaf blades. (Fig. 1, L and M.) As the leaves are relatively broad under such conditions, a single lesion rarely occupies the entire width, so that the organ as a whole remains alive. In lawns cut close and at frequent intervals a much more delicate habit of growth is imposed on the host. A half dozen leaves greatly reduced in size are crowded into an almost rosettelike arrangement. Lesions of only moderate width may extend entirely across the basal part of the blade, thus bringing about its eventual death. (Fig. 2.) A more serious situation results when infection spreads to the closely imbricated delicate leaf sheaths that make up the upper portion of the central axis of the plant. All of the foliar organs, including the very young structures enveloped within, are invaded by the fungus, with the result that the miniature plant is effectually destroyed. (Fig. 3.) In April, 1929, the fairways in the public golf courses in the District of Columbia showed numerous gray or brownish patches in which such destruction was so general that the turf survived only in scattering plants and isolated stools.

That the severe manifestation of the disease in the fairways was caused not only by the prevalence of the parasite, but also by the excessively close cutting to which the grass was subjected, became evident from the fact that the same host in the rough near by, treated less rigorously, appeared in relatively good condition. To be sure, the foliage bore an abundance of lesions, and more than a few leaves were cut off by injuries at the base of the blade, but only occasional plants were killed entirely, and the general appearance of the turf was not noticeably impaired. Undoubtedly, close cutting operates to the disadvantage of the host, not only by imposing a delicate habit of growth especially subject to serious injury by the parasite, but also by entailing an excessive removal of foliage and a consequent loss in capacity for renewed growth. Owing to its generally erect foliar habit, bluegrass is shorn of its leaves in far more rigorous measure than are turf grasses of a more nearly prostrate leaf habit, like creeping bent (*Agrostis stolonifera* L. var. *compacta* Hartm.). The recommendation made by Monteith that when leaf spot is prevalent on Kentucky bluegrass in golf courses the blades of the mower be raised as high as circumstances will permit appears, therefore, to be thoroughly sound.

THE PARASITE

CULTURAL CHARACTERISTICS

As has been suggested previously, *Helminthosporium vagans* can be isolated without difficulty by excising bits of infected host tissue and, after surface sterilization, planting them on a suitable medium like maize-meal agar. Conidia may also be successfully utilized, in spite of the somewhat slow rate of mycelial extension characteristic of the fungus and the greater difficulty incurred thereby from the presence of contaminating bacteria. In cultural characteristics the fungus presents nothing striking enough to set it apart from congeneric types. Zonation involving both aerial and submerged mycelium is not uncommon (fig. 4, A), the darker submerged growth being composed of dark-brown filaments consisting of unusually strongly inflated segments. The tendency toward the formation of densely ramifying

systems, referred to in the earlier account, is emphasized by its growth on Dox agar[9] illustrated in Figure 4, B, and would seem to be associated with retarded growth. That the quantity and the coloration of aerial mycelium is subject to considerable variation not readily traced

FIGURE 2.—A stool consisting of three plants of *Poa pratensis* vigorously attacked by *Helminthosporium vagans*. Many of the leaves are already killed, and those still green bear lesions varying in extent. Photographed from material collected April 30, 1929, in the District of Columbia from a golf course that had been subjected to excessively rigorous cutting. × 3

to any specific cause is shown in Figure 4, C, *a* and *b*, representing two growths obtained in parallel potato-dextrose agar plate cultures. In tube cultures, owing apparently to the moister conditions, flesh-colored columnar structures somewhat resembling those formed by *H. teres* Sacc. and *H. avenae* Eidam frequently make their appearance.

[9] Distilled water, 1,000 c. c.; magnesium sulphate, 5 gm.; dipotassium phosphate, 1 gm.; potassium chloride, 0.5 gm.; ferrous sulphate, 0.01 gm.; sodium nitrate, 2 gm.; dextrose, 5 gm.; agar, 15 gm.

MORPHOLOGY AND TAXONOMY

Although in artificial culture *Helminthosporium vagans* generally remains sterile, occasionally a moderate number of conidiophores and conidia are produced. In some instances the sporophores are represented by the terminal portions of aerial hyphae differentiated somewhat from the vegetative parts by a slightly greater diameter, a

FIGURE 3.—A plant of *Poa pratensis* severely attacked by *Helminthosporium vagans*. The three remaining green leaves are so severely affected at the closely arranged sheaths as to leave no doubt as to their early destruction. Photographed from material collected April 30, 1929, in the District of Columbia, from a golf course that had been subjected to excessively rigorous cutting. [×3

thicker wall, and a deeper coloration. More frequently, however, they are present as lateral branches on the longer aerial filaments, modified in the same manner as the terminal conidiophores, the deeper coloration and greater thickness of wall usually extending a short distance into one or both arms of the parent hypha. (Fig. 5, A–H.) These lateral sporophores ordinarily show a range in length from approximately 25μ (fig. 5, C) to over 100μ (fig. 5, G), and a range in

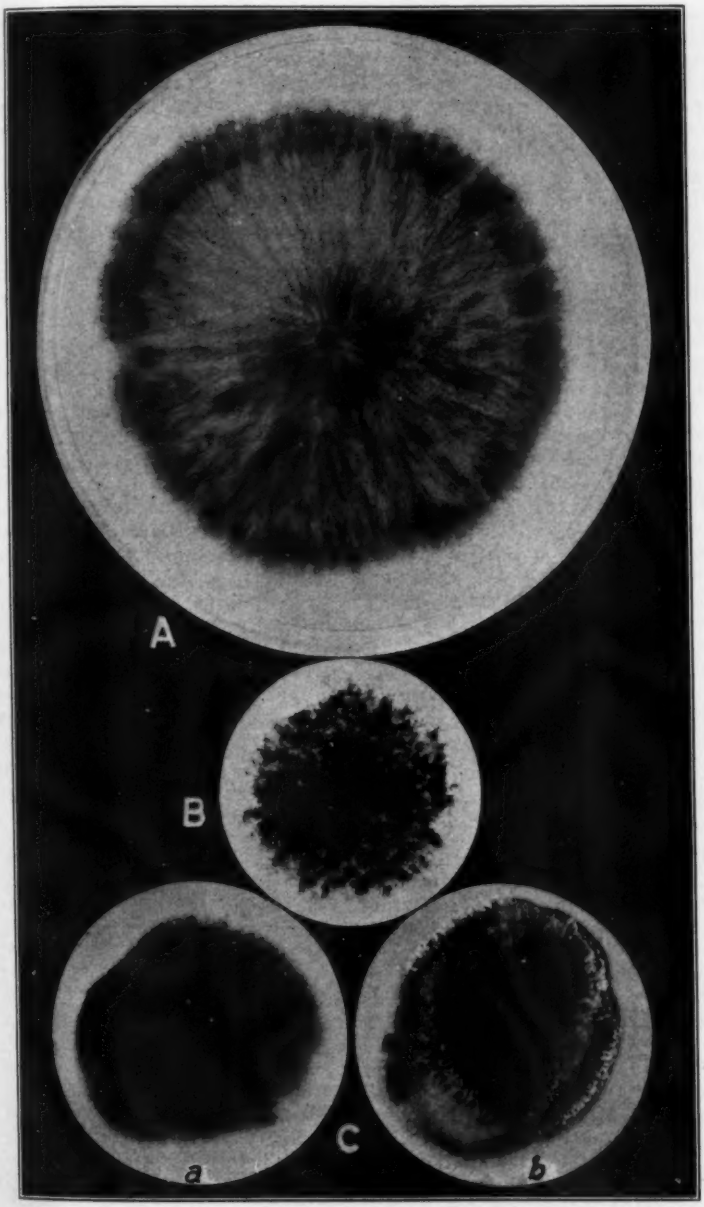

FIGURE 4.—Growth of *Helminthosporium sagans* in plate culture 12 days after planting: A, Maize-meal agar; B, Dox agar; C, potato-dextrose agar. The ready variability of the fungus with respect to the appearance of the aerial mycellium is shown in C, *a* and *b*, representing parallel cultures of the same age and on the same substratum. ×1

number of septa from one (fig. 5, C, and H, *a*) to five (fig. 5, G). Most conidiophores give rise to only one conidium (fig. 5, A–E), but instances in which continued development results in the production of a second spore are not rare (fig. 5, F, *a*, *b*, and G, *a*, *b*). The lateral sporophores are usually inserted on the parent filament at rather long intervals, though cases of more closely approximated origins occur. (Fig. 5, H, *a* and *b*.) The conidia produced in culture on artificial media resemble in general shape those found in nature. With respect to coloration they are generally somewhat darker, because of a larger proportion of olivaceous individuals than yellowish or brownish ones. Especially marked, however, is their inferiority in size and number of septa, as is evident by a comparison of the conidia shown in Figure 5, A–H, with those shown in Figure 5, I–S, the latter having been drawn at the same magnification from field material. Such inferiority, to be sure, is generally characteristic of most of the species of Helminthosporium parasitic on grasses that can be induced to sporulate at all in artificial culture.

In this connection attention is directed to certain of the more extreme expressions of morphological features pertaining to conidia produced under natural conditions. The conidium represented in Figure 5, L, for example, exhibits 12 septa, 2 in excess of the number allowed for in the original diagnosis. The one shown in Figure 5, J, was found to measure 137μ in length, while the spores represented in Figure 5, P and S, measured 25μ in diameter—magnitudes also somewhat in excess of those previously submitted. In order that undue importance may not be assigned to such extreme values, it may not be amiss to include here a brief summary of measurements of lengths and diameters made on 200 living conidia selected at random in mounts of material scraped from Kentucky bluegrass leaves collected on a golf course in the District of Columbia on May 1, 1929. The 200 measurements of spore lengths fall into classes covering range intervals of 5μ, as follows: 31–35μ, 3; 36–40μ, 3; 41–45μ, 4; 46–50μ, 6; 51–55μ, 3; 56–60μ, 4; 61–65μ, 14; 66–70μ, 13; 71–75μ, 21; 76–80μ, 18; 81–85μ, 25; 86–90μ, 26; 91–95μ, 17; 96–100μ, 13; 101–105μ, 11; 106–110μ, 7; 111–115μ, 2; 116–120μ, 5; 121–125μ, 2; 126–130μ, 1; 131–135μ, 0; 136–140μ, 2. The corresponding 200 measurements of spore diameters are referable to the different values found, as follows: 11μ, 1; 12μ, 1; 13μ, 1; 14μ, 1; 15μ, 4; 16μ, 5; 17μ, 25; 18μ, 40; 19μ, 41; 20μ, 38; 21μ, 19; 22μ, 10; 23μ, 8; 24μ, 3; 25μ, 3. Counts of cross walls made on the same 200 individual conidia are distributable as follows: 2 septa, 3; 3 septa, 8; 4 septa, 21; 5 septa, 34; 6 septa, 39; 7 septa, 46; 8 septa, 28; 9 septa, 14; 10 septa, 4; 11 septa, 1; 12 septa, 2. Computations from the three sets of values for the 200 spores gave 82.7μ as the average length of the conidium, 19.1μ as the average diameter, and 6.3 as the average number of septa. The conidium shown in Figure 5, I, thus represents a moderately close approximation to the average values determined from field material, though comparing more than favorably with the largest individual spores produced in artificial culture.

While conidia of members of genus Helminthosporium do not regularly exhibit septa other than transverse cross walls, oblique and even longitudinal partitions occur rather sparingly in most species. Such departures from the usual morphological trend are present also in conidia of *Helminthosporium vagans*. Oblique partitions are not

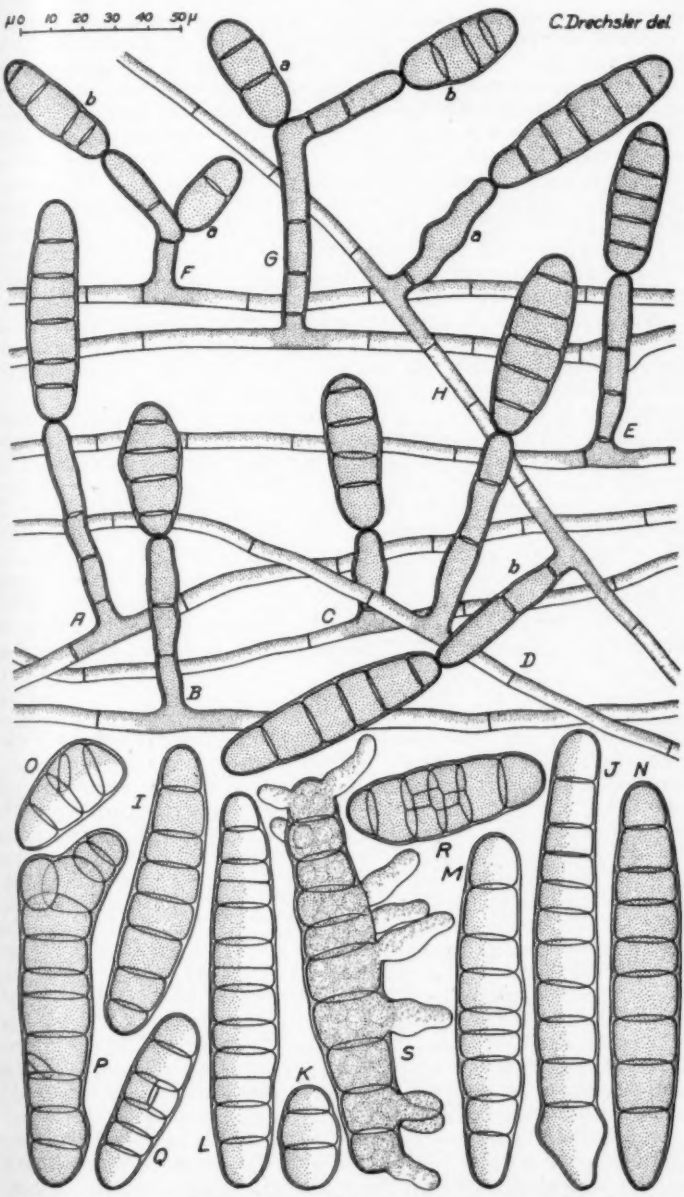

FIGURE 5.—A–H, Portions of aerial filaments of *Helminthosporium vagans* bearing conidiophores with one or two conidia. Drawn from material produced in a 30-day-old maize-meal agar plate culture. × 500. I–S, Conidia of *H. vagans* from affected leaves of *Poa pratensis* collected in Washington, D. C., May 1, 1929. Note the germination of S by the production of germ tubes from intermediate as well as from end segments. × 500

infrequently associated with marked curvature in the axis of the spore, though in many instances their presence, like that of longitudinal septa for the most part, is independent of any unusual external feature. The occurrence of one or two septa of the latter type, especially in conidia of the smaller dimensions, brings about a striking resemblance to ascospores of certain species of Pyrenophora having a Helminthosporium stage parasitic on grasses. The resemblance is of interest especially because the germination of the conidia by the production of germ hyphae indiscriminately from the intermediate as well as from the end segments (fig. 5, S) indicates that *H. vagans* is indeed to be regarded as belonging to that series of forms achieving their sexual stage in the ascigerous genus mentioned, or in the very closely related, if not identical, genus Pleospora Fries. That the muriformly septate bodies in question were actually conidia rather than ascospores was sufficiently apparent in that they were regularly provided at one of the ends with a scar entirely like the basal scar invariably present in the more regularly partitioned conidia of the leaf-spot fungus, and marking the point of their former attachment to the conidiophore.

Owing to the exceptionally early appearance of the leaf spot on Kentucky bluegrass in 1929, with the resulting occurrence of the causal parasite in quantity on new growth while the withered remains of growth of the previous season were still intact, opportunity for the discovery of an ascigerous stage of *Helminthosporium vagans* might well be considered as having been favored in at least one respect. Some effort was therefore made to detect perithecia that might plausibly represent a phase in the life history of the parasite. However, no perithecial form occurring in a relationship suggesting an ontogenetic connection was found in any of the decaying material examined.

SUMMARY

Helminthosporium vagans, previously set forth as a relatively innocuous parasite on *Poa pratensis*, has at various times during several seasons been found to cause conspicuous damage, especially in the fairways of golf courses. The most destructive effects occur apparently when the grass has been subjected to close cutting. The delicate habit of growth encouraged thereby results in plants with the upper axial part consisting mostly of imbricated leaf sheaths of such small proportions as to be subject to direct destruction through the development of foot-rot lesions. The excessive reduction of functional leaves resulting from close clipping because of the erect foliar habit of the grass evidently reduces the capacity for renewed growth. The few field observations made by the writer confirm the validity of the recommendation of less drastic mowing as preventive and remedy.

In pure culture the fungus occasionally produces conidia resembling the smaller ones produced under natural conditions, the conidiophores being represented by noticeably differentiated terminal prolongations or lateral branches of aerial filaments. The germination of the conidia by germ tubes arising from middle as well as from end segments indicates close affinity of the fungus with the series of graminicolous congeners achieving their ascigerous phase in the genus Pyrenophora, although no sexual stage of any kind has yet been found associated with it.

WOOL FINENESS AS INFLUENCED BY RATE OF GROWTH [1]

By J. I. HARDY, *Senior Animal Fiber Technologist*, and J. B. TENNYSON, *Junior Animal Fiber Technologist, Animal Husbandry Division, Bureau of Animal Industry*

INTRODUCTION

A study of the variations in the fineness of individual wool fibers as they grow has revealed facts that are of practical significance to the flockowner and the wool trade. According to Roberts [2] "fineness is one of the most important properties of wool." Fleeces with good, sound, uniform fibers bring a better return to the woolgrower and are more desired by the wool manufacturer than those showing undesirable irregularities in diameter along their length. Such well-grown, uniform fleeces make possible the production of cloth of better quality than is possible with similar fleeces produced under poor growing conditions.

Close examination of a large number of fleeces under varying conditions of sheep management has led to the belief that the fineness of wool fibers throughout the growing period of a fleece is affected by the conditions of feeding, breeding, and management under which the wool has been grown. Testing for strength of staple with the fingers has indicated that there is considerable difference in fleeces that appear to be of the same fineness. One often finds wool at shearing time that is weak at some point in the staple and will break under a slight strain. This condition of the wool may have been caused by sickness or other adverse conditions, which in many cases might have been avoided by better management of the sheep.

Roberts [3] refers to the "rise" or thinning of fibers which takes place just before shearing as an intermediate condition of shedding. When this condition occurs it may be caused by hereditary factors. A wool merchant may buy a considerable quantity of staple wool and find many fleeces in the lot that are weak, a condition referred to by the trade as "tender." When these wools are tested for staple strength they yield quickly at one well-defined line across the staple. A small staple is often so weak in one place that, when held horizontally, it will bend over from its own weight. The wool from these tender fleeces is not suitable for combing and the fleeces are, therefore, usually put in with the clothing grades. Sometimes this weak or tender place in the wool occurs a short time before shearing and at a point so near the end of the wool fibers that there is still sufficient length of wool to comb into tops. However, there is a smaller yield of long fibers from these fleeces and they are, therefore, not so profitable to the manufacturer.

[1] Received for publication Oct. 5, 1929; issued March, 1930.

[2] ROBERTS, J. A. F. WOOL RESEARCH AND THE FARMER. Brit. Research Assoc. for Woollen and Worsted Indus. Pub. 103, 16 p. 1928.

[3] ROBERTS, J. A. F. Op. cit., p. 10.

PRELIMINARY OBSERVATIONS

In the fall of 1924 the senior writer visited a number of wool houses in Boston and obtained samples of tender wool in order to secure information that would help to overcome this defect. In a study of these samples a thinning out of the fibers was readily observed, but there was difficulty in finding a tender place in a fiber that was entirely within the field of the microscope when it was magnified about 150 diameters. A sample of wool obtained from a very tender Australian fleece had an abrupt change in the diameter of the fibers. Figure 1 illustrates such a weak place or "break" in the sample, and

FIGURE 1.—A "break" in a staple. The wool is partially pulled apart to show the location of the weak spot. Approximately natural size

Figure 2 is a microphotograph of fibers from the same fleece. These fibers, which are tender and have a very small diameter at one point, show no indications of having ceased to grow.

Weak places in staple wool may be evident in varying degrees according to the reduction in the diameter of the fibers during the period the weak portion of the fiber was growing. Sometimes a sheep may be subjected to such severe conditions that the wool appears to stop growing for a short time. Later, when the sheep becomes thrifty, new fibers apparently are formed in the wool follicle. As these new fibers grow they become embedded in the old ones. This condition is shown in Figure 3. The old fiber will separate from the new fiber under the slightest strain. The sample from which this fiber was taken was obtained from a Southdown sheep seriously infested with internal parasites. All the samples mentioned above, except the last, were warehouse samples of which the previous history

was not available, hence there was no direct information on the cause of formation of the tender wool.

EXPERIMENTAL PROCEDURE

METHOD OF OBTAINING SAMPLES

In order to study wool fineness as influenced by the wool's rate of growth, the writers selected five healthy Corriedale ewes all of which

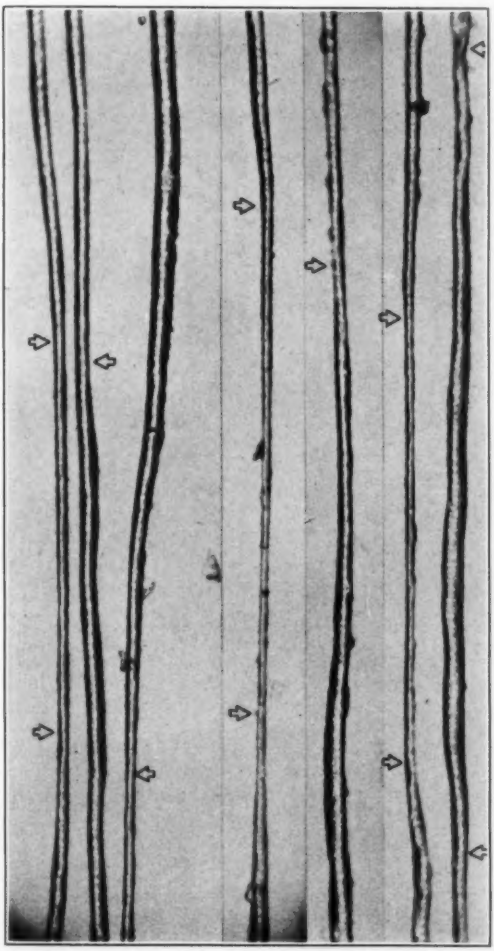

FIGURE 2.—Photomicrograph of fibers taken from lock of wool shown in Figure 1. The weak places in the fibers which have noticeably reduced diameters are indicated by arrows. ×140

produced lambs each year with the exception of sheep 1125 in 1928. The ages of these sheep varied from 1 to 4 years at the beginning of this experiment. Under the supervision of C. G. Potts, of the bureau, these sheep were weighed individually every two weeks and an accurate record was kept of their breeding and feeding.

Wool-growth clippings were obtained from these sheep at 28-day intervals, in the following manner: All the fibers were removed from an area about one-half inch square, located about 3 inches to the rear of the point of the shoulder and midway between back and belly. This area was selected since previous study had shown wool from this portion to be fairly typical of the entire fleece. Twenty-eight days later two small samples of wool, representing the growth during that period, were taken from the same area. The remaining fibers on the area were removed with sharp scissors that cut very close to the skin. The operation was repeated every 28 days. On the same dates that fiber clippings were taken, two small locks of wool were tied with dental floss close to the skin on the right and left side of the same

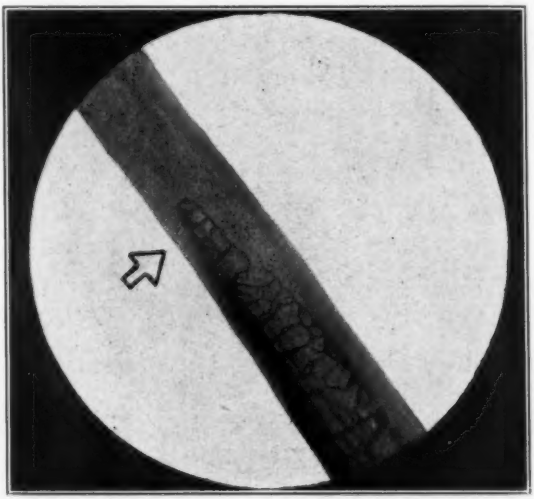

FIGURE 3.—Photomicrograph of the juncture between new and old growths in a wool fiber; the fiber is very weak at such places. × about 500

sheep. Figure 4 illustrates the appearance of the tied locks. These locks made it possible to study the growth of individual wool fibers during successive 28-day periods.

LABORATORY METHODS OF MEASUREMENT

The lengths of the wool clippings were measured with a binocular microscope magnifying 7.5 diameters. This was accomplished by first placing a few of the fibers on a piece of thin glass beneath which was a sheet of cross-section paper of the same size, ruled in millimeters. A microscope slide was then placed across the fibers even with one of the lines of the cross-section paper. The fibers were then pulled slowly out from beneath this slide with small tweezers. When a fiber was just free from the microscope slide, the movement of the tweezers was stopped and the length of the fiber was read to the nearest millimeter. Five fibers were measured from the left and five from the right side of each sheep. The diameter of the wool fibers was meas-

ured with a micrometer caliper having a ratchet stop and graduated to one four-hundredth of a millimeter.

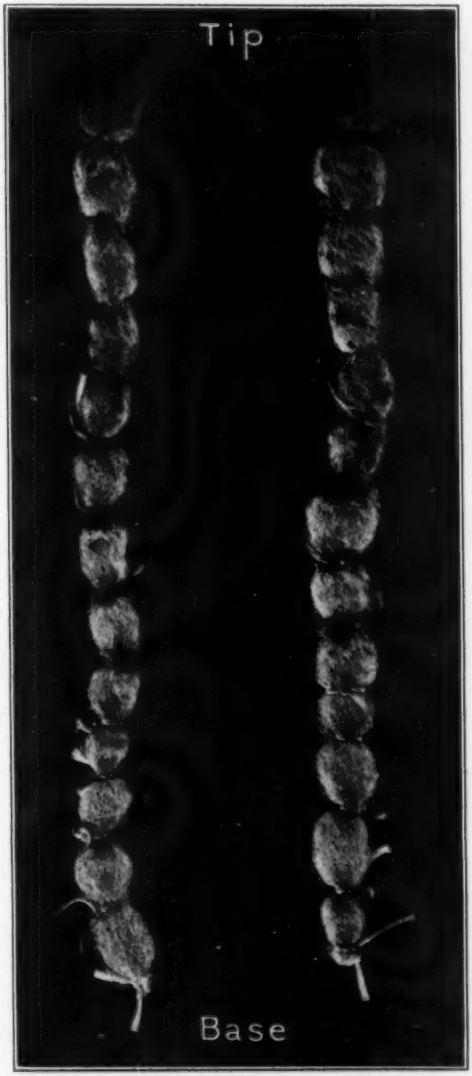

FIGURE 4.—Tied locks showing one year's growth of wool from Corriedale sheep by 28-day intervals. Actual size

Fifty fibers were used for diameter measurements from clippings and tied locks from the left side of each sheep, and 50 from the right. This number was considered sufficiently large to furnish a repre-

sentative average of the samples. Portions representing the same growth period of 25 fibers from the left and from the right side samples of each sheep were measured both with the micrometer caliper and with a microprojector in order to compare the results by these two methods. Under the conditions, this number was considered sufficient to show an accurate comparison between the two methods. By means of the microprojector, the fibers were projected with a 1,000-diameter magnification on an aluminum-coated screen. The measurements on the screen were made with a scale graduated in millimeters. With this magnification each millimeter of the image, as projected on the screen, represented 1 micron of actual wool fiber.

FIGURE 5.—Tied lock of wool with alternate portions dyed to show the different growth periods. Actual size.

The length and diameter of clippings from the greatest, least, and last growth periods of the year 1927–28 were again measured in order to study the relationship of length and diameter to weight. For this purpose 100 fiber clippings were taken from the left and right sides of each sheep. This larger number of fibers was used in order to have a quantity that could be weighed with accuracy. After the length of each fiber was determined, its diameter also was immediately measured with a micrometer caliper. The weights of each of these groups of 100 fibers were taken on a microbalance and the fibers were then placed in small gelatine capsules for safe keeping and future reference.

All measurements were made under controlled conditions of temperature and humidity with the exception of those taken by means of the microprojector. Owing to the heat caused by the operation of the microprojector, it was impossible to maintain a constant temperature while making these measurements. For all other measurements the temperature was maintained at 70° F. and the relative humidity was kept at 65 per cent.

The various growth periods on the tied locks were shown more clearly by dyeing alternate growth periods as illustrated in Figure 5. This was accomplished by wrapping a thread saturated in crude wool grease around the growth of alternate 28-day periods so that it covered the entire growth of such periods; the greased thread excluded the dye from the covered portions of the

lock. The entire lock was then dyed in an alcoholic solution of malachite green dye just long enough to stain all the fibers of the unprotected growth periods.

After the wool-growth clippings and tied locks were measured for length, tabulations were made of the data on the basis of average length growth for the five sheep from the periods in which the wool grew the greatest length, the least length, and also for the last growth period before shearing. These measurements, from samples obtained from each of the five animals for four successive years, are presented in Table 1. The average diameter of the growth clippings for the same periods is also given. In four cases the greatest and least growth periods for individuals are not the same as that for the average of the group. These variations were largely due to differences in the dates of lambing and other factors influencing the physical condition of the sheep. The coarsest fibers were produced each year during the periods of greatest growth and the finest during those of least growth.

TABLE 1.—*Average length and diameter of 100 wool fibers, for the greatest, least, and last growth periods, for five Corriedale sheep during four successive years*

Sheep No.	For greatest growth period, 28 days ended Aug. 28, 1925		For least growth period, 28 days ended Jan. 12, 1926		For period just before shearing, 28 days ended May 4, 1926		For greatest growth period, 28 days ended Oct. 20, 1926	
	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter
	Cm.	*Microns*	*Cm.*	*Microns*	*Cm.*	*Microns*	*Cm.*	*Microns*
977	1.27	22.75	1.06	21.78	1.12	16.90	1.40	25.00
979	1.47	22.98	1.08	21.95	1.24	20.33	1.48	23.83
982	1.21	22.80	.92	19.78	1.18	20.98	1.19	26.18
1125	1.50	20.08	.90	17.70	1.50	19.98	1.49	22.95
2B	1.55	28.00	1.01	24.38	1.16	24.33	1.56	28.70
Average	1.40	23.32	.99	21.12	1.24	20.50	1.42	25.33

Sheep No.	For least growth period, 28 days ended Jan. 12, 1927		For period just before shearing, 28 days ended Apr. 6, 1927		For greatest growth period, 28 days ended June 29, 1927		For least growth period, 28 days ended Feb. 8, 1928	
	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter
	Cm.	*Microns*	*Cm.*	*Microns*	*Cm.*	*Microns*	*Cm.*	*Microns*
977	1.18	23.95	1.12	21.48	1.46	25.58	1.10	18.13
979	1.14	23.90	1.20	23.68	1.37	26.68	.98	21.58
982	1.05	25.00	1.23	25.03	1.22	27.08	1.05	21.05
1125	1.24	22.08	1.27	22.88	1.35	26.28	1.15	20.25
2B	1.30	27.58	1.13	23.25	1.37	30.05	1.02	26.70
Average	1.18	24.50	1.19	23.26	1.35	27.13	1.06	21.54

Sheep No.	For period just before shearing, 28 days ended May 1, 1928		For greatest growth period, 28 days ended Oct. 17, 1928		For least growth period, 28 days ended Feb. 6, 1929		For period just before shearing, 28 days ended May 1, 1929	
	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter
	Cm.	*Microns*	*Cm.*	*Microns*	*Cm.*	*Microns*	*Cm.*	*Microns*
977	1.16	23.00	1.28	23.80	1.08	22.13	1.25	23.15
979	1.15	23.15	1.26	24.20	1.10	22.68	1.14	21.05
982	1.12	23.33	1.10	24.63	.88	21.33	1.09	23.08
1125	1.27	23.73	1.32	22.03	1.11	22.83	1.13	24.18
2B	1.38	27.88	1.35	29.68	.99	25.70	1.21	27.83
Average	1.22	24.22	1.26	24.87	1.03	22.93	1.16	23.86

TABLE 2.—*Comparison of average diameters of 100 wool fibers from tied locks of five Corriedale sheep, measured with a micrometer caliper and also by a microprojector*

Sheep No.	Average diameter of 100 wool fibers—					
	For greatest growth period, 28 days ended June 29, 1927,[a] when measured with—		For least growth period, 28 days ended Feb. 8, 1928,[b] when measured with—		For period just before shearing, 28 days ended May 1, 1928,[c] when measured with—	
	Micrometer caliper	Microprojector	Micrometer caliper	Microprojector	Micrometer caliper	Microprojector
	Microns	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*
977	25.28	26.66	19.10	20.50	21.83	24.74
979	24.98	28.08	20.35	22.64	21.58	26.20
982	27.23	30.42	20.98	23.68	22.25	24.56
1125	25.80	29.32	17.58	23.12	23.68	28.56
2B	31.03	34.36	26.03	30.04	27.75	30.72
Average	26.86	29.77	20.81	24.00	23.42	26.96

[a] Average length of clippings, 1.35 cm.
[b] Average length of clippings, 1.06 cm.
[c] Average length of clippings, 1.22 cm.

The measurements of diameter which were taken with a micrometer caliper and also with a microprojector are recorded in Table 2 and

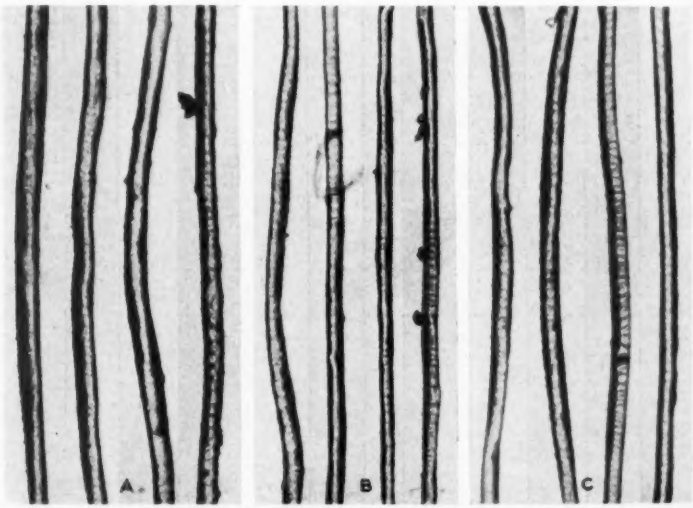

FIGURE 6.—Photomicrographs of four wool fibers as they appeared during their greatest (A), least (B), and last (C) growth periods. × 140

Figure 6 is a microphotograph of four wool fibers showing portions of their greatest, least, and last wool growth periods. The measurements made with the micrometer caliper were consistently lower than those made with the microprojector. In order to determine the cause of these differences in the diameter measurements, 25 short pieces of fine uniform wire were measured by both methods. The average

diameter for the wire with the micrometer caliper was 82.80 microns and with the microprojector was 85.64, a difference of 2.84 microns. The average differences found between the measurements made with the micrometer caliper and the microprojector in the case of the wool fibers was 3.21 microns. Thus with both materials the measurement of fibers by means of the microprojector gave results slightly greater than those obtained with the micrometer caliper. The microprojector generally yields more consistent results, however, than the micrometer caliper, and makes possible the more rapid measurement of growth changes in the diameter of wool fibers. It is impossible to use the micrometer caliper for measuring changes occurring quickly because of the width of its jaws which are too large to measure short-time growth.

TABLE 3.—*Average length, diameter, and weight of 100 wool-growth fiber clippings for the greatest, least, and last growth periods of four Corriedale sheep*

Sheep No.	Item	For greatest growth period, 28 days ended June 29, 1927			For least growth period, 28 days ended Feb. 8, 1928			For period just before shearing, 28 days ended May 1, 1928		
		Length	Diameter	Weight	Length	Diameter	Weight	Length	Diameter	Weight
		Cm.	*Microns*	*Mgm.*	*Cm.*	*Microns*	*Mgm.*	*Cm.*	*Microns*	*Mgm.*
977	Left side	1.248	24.95	1.20	0.914	17.85	0.46	1.036	21.88	0.73
	Right side	1.426	24.75	1.28	.984	16.70	.47	1.137	22.30	.77
	Average	1.337	24.85	1.24	.949	17.28	.465	1.087	22.09	.75
	Average weight of 1 cm. growth			.927			.490			.690
979	Left side	1.088	24.00	.94	.917	19.50	.51	1.040	21.50	.71
	Right side	.958	25.30	.80	.896	20.08	.57	1.090	23.00	.79
	Average	1.023	24.65	.87	.907	19.80	.54	1.065	22.25	.75
	Average weight of 1 cm. growth			.850			.595			.704
982	Left side	1.040	26.25	1.10	.840	18.50	.50	.910	20.00	.67
	Right side	1.090	26.50	1.25	.940	18.50	.54	.990	21.50	.79
	Average	1.065	26.38	1.175	.890	18.50	.52	.950	20.75	.73
	Average weight of 1 cm. growth			1.103			.584			.768
1125	Left side	1.250	25.00	1.170	.980	19.48	.64	1.090	24.85	.95
	Right side	1.300	25.75	1.34	1.040	18.95	.60	1.160	24.60	1.02
	Average	1.275	25.38	1.255	1.010	19.22	.62	1.125	24.73	.985
	Average weight of 1 cm. growth			.984			.614			.876
	Average	1.175	25.32	1.135	.939	18.70	.536	1.057	22.45	.804
	1 cm. growth			.964			.571			.760

The average of the length, diameter, and weight of 100 fibers from clippings taken from the left and right sides of four Corriedale sheep are shown in Table 3. The difference in weight of fiber between the greatest and the least wool growth periods for the four sheep was 52.8 per cent. As has been previously stated, the length of the wool-growth periods was 28 days, or one-thirteenth of a year. Based on a 10-pound fleece shrinking 55 per cent, this would mean a reduction of 0.182 pound of clean wool during a period of 28 days. The reduction in length of the wool from the greatest to the least growth period is 2.36 millimeters. For a reduction of 1 millimeter in length (with-

out taking diameter into consideration) there would be a reduction of 0.0771 pound of clean wool. In order to find out what proportion of the decrease in weight of fiber is due to the reduction in diameter, the weights of fiber for each period equivalent to 1 cm. growth were determined. These figures are given in the table opposite the average weight of 1 cm. The reduction in wool diameter from the greatest to the least growth period is 6.62 microns, with a corresponding reduction of 0.393 mgm. of wool fiber. This is equal to 6.11 per cent reduction in weight of wool fiber for each decrease of 1 micron in diameter. With these figures also based on a 10-pound fleece shrinking 55 per cent, there would be a reduction of 0.02 pound of clean wool in 28 days due to reduction in diameter of wool fiber. These data show that there is a reduction in weight of fleece resulting from both the reduced rate of growth and the reduction in fiber diameter.

This group of experimental sheep had better feed and care than most flocks of sheep and did not have to withstand the hardships of range conditions, yet the less favorable conditions in the winter months were reflected directly in their wool production. The wool of these sheep was sound, but not of such good quality as it would have been had it been uniform in diameter throughout its entire length. A reduced rate of growth associated with a reduction of the diameter of wool fiber is the first indication of tender undesirable wool.

DISCUSSION

An analysis of the records for these sheep showed that the greatest wool growth is associated with a thrifty condition of the sheep as indicated by the weight records. The end of the period of least growth of wool was found to be from about 45 days before lambing to about lambing time. After this fact was determined, the data for length of wool grown for the last period before shearing were selected and diameter measurements were made of fibers grown in this period. This was done in order to determine what the diameters of the fibers were during a period as late as possible before shearing.

Probst [4] based a series of measurements on observations of Zorn who stated [5] that wool grows two-thirds of its length in the first six to seven months and one-third of its length in the remaining months of the yearly period between shearings. On this basis, Probst measured a wool sample, from one of his stud bucks, at four different places along its length. He calculated that the measured portion of the tip was produced in August; that of the section next to the tip in October, before breeding time; the measured portion of the third section in December; and that of the base in March or April. He concluded that this decrease probably was due in part to the influence of the winter season and in part to reduced vigor of the buck after breeding time. The decrease, moreover, was more pronounced in 1923 than in 1924; Probst explains this by the fact that in the first instance the buck had run with the flock, while in the second case, hand breeding was practiced.

[4] PROBST, E. DIE FEINHEITSBESTIMMUNG DES WOLLHAARES. Ztschr. Tierzuchtung u. Zuchtungsbiol. 6: [403]–488, illus. 1926.

[5] ZORN, W. HAUT UND HAARE ALS RASSE UND LEISTUNGSMERKMAL IN DER LANDWIRTSCHAFTLICHEN TIERZUCHT. Flugschr. Deut. Gesell. f. Zuchtungsk. 48. 1919. [Original not seen.]

The findings of Duerden and Bosman [6] in their study of wool from seven sheep at three different places along the staple, including the top, middle, and base, show that "the growth of the fleece is less vigorous toward the end of the season than at any other period." It seems quite possible that the end of the season might have been unfavorable for the growth of the fleeces from which those seven samples were taken and that more favorable conditions would have been associated with a larger diameter. It is also possible that the reduced growth, in part, may have been caused by some hereditary factor. The writers' data on the clipping measurements also show that the average diameters for the greatest, least, and last growth periods vary directly with the average rate of growth.

SUMMARY

A study of five healthy Corriedale ewes was undertaken in order to determine, if possible, the effect of the rate of wool growth on fineness and length of fibers. Periodic wool-growth clippings and tied locks were used in this study. It was found that the rate of wool growth and the fineness of the fibers produced varied throughout the year, both growth and coarseness being greatest in summer or fall and least in midwinter. The greatest growth in length of fiber appeared to be correlated with the largest diameter of fiber and vice versa. The period of greatest wool growth was also associated with a generally thrifty condition of the sheep as indicated by their weight. The period of least wool growth occurred, in ewes, usually during lambing time and the 45 preceding days. The weight of the wool fibers increased as the length and diameter increased and vice versa. The indications are that the character of the fleece is probably very largely within the control of the flock owner because the experiments appear to show that there is a rather close relationship between the thriftiness of a sheep and the quality and quantity of wool it produces.

[6] DUERDEN, J. E., and BOSMAN, V. ABSENCE OF UNIFORMITY IN GROWTH OF THE MERINO FLEECE. Jour. Textile Inst. 18: T191–T194, illus. 1927.

THE CHEMICAL COMPOSITION OF COLLOIDAL MATERIAL ISOLATED FROM THE HORIZONS OF VARIOUS SOIL PROFILES[1]

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INTRODUCTION

Investigation of the chemical composition of colloidal material isolated from the soil has been confined largely to that occurring in the upper part of the soil profile; that is, in the A and B horizons. This work has indicated the extent to which soil colloidal material may vary in composition over a large area, namely, the humid portion of the United States, as well as in restricted areas of the same or related soils. It is important, however, especially in connection with the study of soil genesis and profile development that something be known of the composition of colloidal material in the lower part of the profile, in the C horizon, and in the zone of decomposing rock. Although colloids of the A and B horizons of most soils are of similar composition, it is not unlikely that greater differences might be found in colloids in the deeper parts of the profile where nature of the parent material rather than climatic influences would be expected to determine the composition of the colloidal material. Comparison of the composition of colloidal material isolated from the upper soil horizons with that occurring in the lowest horizons should indicate what changes have taken place in the colloid as the result of leaching and aging.

PREVIOUS WORK

The most extensive investigation of the composition of colloidal material isolated from the soil is that reported by Robinson and Holmes (*9*).[2] The investigations of others on the finest fractions of the soil have been reviewed by these writers and need not be considered here. Robinson and Holmes concluded from their study of the colloidal material in the A and B horizons of 15 American soils that the colloids isolated from the surface soil and from the corresponding subsoil are much alike in composition. More recently Holmes (*4*) reached the same conclusion from his study of colloids from the Leonardtown soil. McCool (*8*) has reported partial analyses of colloids from a group of Michigan soils which indicate rather wide variations in certain constituents in the different horizons. Potash appears to increase regularly with depth in the profile. Silica decreases regularly in most of the profiles studied, but in several

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[2] Reference is made by number (italic) to "Literature cited," p. 482.

it increases regularly with depth. Phosphoric acid, lime, magnesia, and soda also show considerable variations which do not appear to follow any definite order.

METHODS

Colloidal material was isolated from the soil essentially as described by Robinson and Holmes and in other publications of this bureau. A diameter of 1 micron was taken as the upper limit of colloidal particles. The colloidal material was isolated quantitatively, and an effort was made to remove all the colloid present that could be dispersed by the method employed. The details of the process are as follows: A 200 to 400 gm. sample of soil material, depending on the quantity of colloid present, was worked by hand to a plastic condition and dispersed in about 50 liters of distilled water. The water was made alkaline to phenolpthalein by ammonia. The suspension was passed through a high-power centrifuge and the colloidal material was concentrated by drawing off the water through Pasteur-Chamberland filter candles. The residue in the centrifuge was dispersed in water as before and centrifuged, the process being repeated until a dispersion of the material in 3 liters of water gave after centrifuging only a slightly opalescent solution. In most cases this final colloidal solution contained 0.1 gm. or less of solid material. In other cases it seemed impossible to reach quite this lower limit. The concentrated colloid was evaporated to dryness on the steam bath.

The isolated colloids and their corresponding soils were analyzed by the fusion method as given by Hillebrand (*3*). Combined water was estimated by deducting from the loss on ignition the organic matter, which was determined as CO_2 by the dry-combustion method, the factor 0.471 being used. Values for organic matter so obtained are, of course, only approximate and in individual cases may vary widely from the true values. Determinations of pH values were made electrometrically.

DESCRIPTION OF WORK

The samples used in this investigation were selected to represent a wide range of soils which have developed under humid conditions. The profiles varied in their characteristics from the Emmet, a typical podsol, to the Barnes identified as Chernozem. The other profiles selected possessed characteristics intermediate between these extremes. They were mainly from the southern part of the piedmont plateau. This region was represented by three soil series, the Cecil, the Porters, and the Durham, the profiles differing chiefly in degree of maturity. The Cecil profile is fully developed, the Porters somewhat less mature, while the Durham profile is immature. These three profiles have developed from gneiss.

A second Cecil profile derived from mica schist was included in this group to bring out possible differences in the composition of colloidal material that may have been induced by a different kind of parent material. A profile of the Houston series, a Rendzina, was also chosen for examination.

The soil samples were selected especially for this and similar investigations by W. E. Hearn and Mark Baldwin of the Division of Soil Survey. It was especially important for this work that the

soils studied should be developed in place from homogeneous parent material. So far as could be judged by color, texture, and general field appearance these profiles were normally developed and had not recently been disturbed.

A description of the profile samples is given in Table 1. Although certain horizons only of each profile were studied, descriptions of the complete profile are given.

TABLE 1.—*Description of the soil profile samples*

Profile No.	Soil type	Depth in inches	Horizon	Description	Parent material	Location
1	Emmet fine sandy loam.	0 - 1	A_0	Litter and sandy humus soil	Glacial drift.	Menominee County, Mich.
		1 - 4	A_1	Whitish-gray fine loamy sand		
		4 - 12	B_1	Yellowish, mellow, friable, light fine sandy loam.		
		12 - 24	B_2	Mottled gray, yellow, and brown, porous, brittle, slightly cemented clayey sand.		
		24 - 33	B_3	Brown, porous, brittle, gritty, light sandy clay.		
		33 - 48	C_1	Pale, purplish-gray light drift		
		48 - 60	C_2	Pinkish-gray, gravelly, light sandy clay drift.		
2	Cecil clay	0 - 5	A	Reddish-brown clay loam	Gneiss	Rutherford County, N. C.
		5 - 36	B_1	Red, stiff, brittle clay		
		36 - 72	B_2	Red, friable, micaceous clay		
		72 - 96	C_1	Brownish-red, friable, partly decomposed rock.		
		96 -112	C_2	Gray, soft, disintegrated rock		
		112+	C_3	Soft rock		
3	Cecil sandy clay loam.	0 - ½	A_0		Mica schist.	DeKalb County, Ga.
		½- 4	A_1	Reddish-brown loamy fine sand		
		5 - 8	A_2	do		
		9 - 16	B_1	Red, friable fine sandy clay		
		17 - 22	B_2	do		
		23 - 62	B_3	Red, heavy clay		
		63 - 85	C_1	Red, decomposed rock		
		86 -108	C_2	Yellowish-red, partly decomposed rock		
		120 -168	C_3	Yellow, partly decomposed rock		
		180 -198	C_4	Grayish-brown disintegrated rock		
4	Porters loam.	0 - 4	A	Brown loam	Gneiss	Rutherford County, N. C.
		4 - 14	B_1	Reddish-brown clay loam		
		14 - 48	B_2	Reddish-brown, friable clay		
		48 - 60	C_1	Reddish-yellow, partly decomposed rock.		
		60 - 72	C_2	Gray, disintegrated rock		
		72 - 96	C_3	Light gray, partly disintegrated rock		
		96+		Bedrock		
5	Durham sandy loam.	0 - 7	A	Light-gray, loose sandy loam	Granite.	DeKalb County, Ga
		19 - 36	B_1	Light, mottled, yellowish-brown sandy clay loam.		
		37 - 50	B_2	do		
		51 - 73	C_1	Mottled yellowish-red and yellow and gray partly decomposed rock.		
		74 - 90	C_2	Light-gray and yellow partly decomposed rock.		
		91 -102	C_3	Very light gray, slightly decomposed rock.		
		130 -110	C_4	do		
		110+		Bedrock		
6	Houston clay.	0 - 4	A	Brown silty clay loam	Marl	Dallas County, Ala.
		5 - 36	B	Mottled gray, red, yellow, and yellowish-brown, heavy plastic silty clay.		
		37 - 68+	C	Grayish-yellow, heavy, plastic silty clay		
7	Barnes silt loam.	0 - 2½	A_0	Black silt loam	Glacial drift.	Brown County, S. D.
		2½- 7	A_1	do		
		8 - 11	A_2	Dark-brown silt loam		
		11 - 14	B_1	Light-brown silt loam		
		14 - 48	B_2	Yellow silt loam		
		28 - 40	B_3	do		
		44 - 56	C_1	Brown, yellow, and gray mottled drift		
		60 - 78	C_2	do		

CHEMICAL COMPOSITION OF SOILS AND ISOLATED COLLOIDS

The chemical composition of the soils from which the colloidal materials were removed are shown in Table 2. The percentages of colloid isolated and the pH value of each horizon are also shown in the table. In the case of two profiles, Nos. 4 and 5, the composition of the fresh parent rocks is given.

The analyses of the soils indicate in most cases marked accumulation of sesquioxides in the B horizons of all profiles except Nos. 6 and 7, with corresponding reduction in the percentages of silica. These high percentages of iron and alumina are accompanied by increases in percentage of combined water, indicating, of course, concentration of the products of decomposition. The percentages of isolated colloid (column 5) parallel in general the increases in sesquioxides and combined water with certain exceptions. For instance, the quantities of iron, alumina, and combined water are as high in the lower parts of the C horizon of profile No. 3 as they are in the B horizon, although the quantity of colloid removed from these lower horizons is only one-sixth to one-seventh of that removed from the B horizon. This might indicate that relatively little colloid in these lower horizons was removed or that the colloid was unusually high in sesquioxides and combined water. The most probable explanation, however, is that the mineral portion of the C horizon of this profile is composed almost entirely of highly altered muscovite and biotite which, as shown by a previous paper (*2*), contain within the mica particle varying amounts of material higher in alumina and water than the fresh mica.

A similar high proportion of alumina and water is shown by the sample from horizon C_4 of profile No. 5 in which the percentages of alumina and water are wholly out of proportion to the quantity of colloid isolated from this horizon. In view of the presence of material in mica particles having substantially the composition of colloidal soil material, it is possible that the feldspar particles, of which the horizon in question is chiefly composed, contain somewhat large amounts of material approaching soil colloidal material in composition.

That a degree of weathering has taken place in the transition of the fresh granite of profile No. 5 to the partially decomposed material of the C_4 horizon that is out of proportion to the quantity of colloid removed is also indicated by the low pH value of this horizon, 5.47, and by the fact that at least 38 per cent of the silica originally present in the fresh rock has been lost. In fact, the relatively low pH values of the partially decomposed parent rock in profiles Nos. 2, 3, and 4, which are 4.83, 4.90, and 5.47, respectively, indicate more extensive decomposition than the appearance of the material or the quantity of colloid would indicate. Extensive alteration of the soda feldspars in particular is indicated by the marked reductions in soda which have occurred in the breaking down of the parent rock in profiles Nos. 2, 4, and 5.

The compositions of the isolated colloids are shown in Table 3.

TABLE 2.—*Percentage composition and pH values of soils from which colloids (expressed in per cent) were isolated*

Profile No.	Soil type and location	Depth in inches	Horizon	Quantity of colloid isolated	pH	SiO_2	TiO_2	Fe_2O_3	Al_2O_3	MnO	CaO	MgO	K_2O	Na_2O	P_2O_5	Ignition	Organic matter	Combined water	CO_2 from carbonates
*1	Emmet fine sandy loam, Michigan.	1 - 4	A_1	0.7	5.80	86.18	0.49	1.79	5.67	0.09	0.54	0.18	2.61	0.74	0.05	1.32	1.12	0.20	0
		24 - 33	B_2	14.1	6.53	76.46	.48	5.05	9.28	.07	1.85	1.65	2.64	.72	.09	2.00	.41	1.59	0
		48 - 60	C_2	3.0	8.60	71.94	.23	1.93	4.86	.06	6.54	3.90	2.04	.44	.03	8.10	[b].00	1.43	6.67
2	Cecil clay loam, North Carolina	0 - 5	A	21.5	4.80	64.64	1.81	4.80	15.60	.07	.18	.72	2.62	.38	.09	9.34	3.80	5.54	0
		5 - 36	B_1	59.7	5.13	46.00	1.54	11.06	27.26	.05	.18	.67	1.40	.64	.10	11.59	.80	10.79	0
		72 - 96	C_1	27.0	5.47	47.04	1.80	9.92	24.80	.15	.64	2.28	3.14	.68	.68	8.68	.43	8.25	0
		112+	C_3	3.9	4.83	55.72	.95	4.48	22.12	.10	2.54	1.48	5.16	2.94	1.21	3.08	.08	3.00	0
3	Cecil sandy clay loam, Georgia	½ - 4	A_1	5.4	4.87	84.59	.80	3.63	6.92	.02	.10	.40	1.04	.24	.31	2.45	.95	1.50	0
		17 - 22	B_2	37.5	4.73	64.56	.96	7.15	18.54	.02	.06	.22	1.16	.28	.26	6.81	.33	6.48	0
		86 -108	C_2	5.3	5.13	62.73	.71	7.46	19.26	.10	.08	1.22	1.00	.26	.29	7.67	.15	7.52	0
		180 -198	C_4	6.5	4.90	61.06	.74	6.82	19.29	.16	.04	2.15	2.41	.62	.10	6.82	.08	6.74	0
4	Porters loam, North Carolina	0 - 4	A	11.0	4.68	73.00	.53	2.24	11.67	.03	.84	.52	4.28	1.28	.06	6.24	3.97	2.27	0
		14 - 48	B_1	36.6	5.05	60.34	.65	4.92	21.07	.04	.24	.80	3.14	.60	.08	8.02	.46	7.56	0
		72 - 96	C_3	5.2	5.10	67.56	.56	3.52	16.54	.07	.28	.74	5.30	.84	.08	4.22	.09	4.13	0
		96+	Bedrock.	.....	7.65	71.50	.39	2.72	14.21	.05	1.84	.61	4.52	2.84	.42	.44	.06	.38	0
5	Durham sandy loam, Georgia	0 - 7	A	2.9	5.52	79.33	.15	1.02	10.87	.02	.33	.06	5.15	1.01	.26	2.28	.86	1.42	0
		51 - 73	C_1	15.7	4.67	68.28	.14	2.04	19.04	.02	.19	.24	4.94	.40	.15	4.91	.27	4.64	0
		91 -102	C_3	1.7	5.10	70.51	.08	1.02	17.46	.02	.24	.18	6.22	.52	.32	3.85	.19	3.66	0
		103 -110	C_4	2.8	5.47	64.06	[c]	.69	21.46	[c]	.22	.13	5.48	.94	.25	6.98	.20	6.78	0
		111+	Bedrock.	.....	[d]	73.48	.12	.91	15.24	.03	.40	.34	4.28	4.46	.30	.61	.06	.56	0
6	Houston clay, Alabama	0 - 4	A	52.1	4.90	63.81	1.02	7.15	16.25	.09	1.04	1.00	1.16	.30	.66	8.21	2.45	5.76	0
		5 - 36	B	65.1	4.73	61.14	.97	7.76	18.91	.03	1.14	1.24	1.12	.30	.36	7.76	1.19	6.57	0
		37 - 68	C	64.7	5.60	58.44	.92	7.82	20.54	.03	1.66	1.42	1.32	.20	.52	7.87	.62	7.25	0
*7	Barnes silt loam, South Dakota	0 - 2½	A_0	22.8	6.40	70.74	.48	3.36	9.55	.14	1.66	.96	2.11	1.80	.26	10.16	7.30	2.86	0
		14 - 48	B_2	20.2	7.22	72.76	.60	3.95	11.73	.11	1.31	1.27	1.93	1.41	.13	4.49	1.68	2.81	0
		60 - 78	C_2	11.3	8.45	68.64	.44	2.83	9.19	.08	5.13	2.77	1.62	1.60	.11	7.00	[b].00	1.13	5.87

[a] The writer is indebted to G. Edgington for the complete analyses of the samples from horizons A and B, profile No. 1, and for determinations of P_2O_5, MnO, K_2O, Na_2O, and CO_2 as carbonates in the samples from profiles Nos. 1 and 7.

[b] The small amounts of organic matter in these horizons could not be detected by the method used in the presence of large amounts of carbonate.

[c] Trace.

[d] Not determined.

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TABLE 3.—*Percentage composition and pH values of colloidal materials (expressed in per cent) isolated from the horizons of various soil profiles*

Profile No.	Soil type and location	Depth in inches	Horizon	Quantity of colloid isolated	pH of soil	SiO_2	TiO_2	Fe_2O_3	Al_2O_3	MnO	CaO	MgO	K_2O	Na_2O	P_2O_5	Ignition	Organic matter	Combined water	CO_2 as carbonates
[a] 1	Emmet fine sandy loam, Michigan.	1 - 4	A_1	0.7	5.80	41.10	0.90	6.46	19.67	0.44	1.54	1.92	2.09	0.26	0.29	25.81	15.18	10.63	0
		24 - 33	B_3	14.1	6.53	42.53	.76	13.31	21.02	.20	1.05	3.09	2.74	.20	.32	14.16	3.15	11.01	0
		48 - 60	C_2	3.0	8.60	41.46	.60	11.66	13.21	.10	6.69	6.52	3.46	.41	.27	15.32	2.38	5.92	7.02
2	Cecil clay loam, North Carolina	0 - 5	A	21.5	4.75	31.69	.90	10.81	29.61	.11	.42	.87	.87	.33	.35	24.65	10.86	13.79	0
		5 - 36	B_1	59.7	5.13	32.44	1.10	13.73	34.71	.05	.26	.53	.63	.28	.25	16.33	2.54	13.79	0
		72 - 96	C_1	27.0	5.37	28.20	1.12	10.03	38.21	.15	.24	.70	.74	.32	.84	19.82	3.76	16.06	0
		112+	C_3	3.9	4.83	26.42	.46	4.40	37.30	.08	.42	1.33	1.43	.24	3.44	24.30	9.85	14.50	0
3	Cecil sandy clay loam, Georgia	½- 4	A	5.4	4.87	31.30	1.01	11.66	33.64	.07	.56	.78	1.71	.58	.24	18.12	6.33	11.79	0
		17 - 22	B	37.5	4.73	29.90	1.14	14.05	36.60	.04	.46	.66	1.28	.54	.35	15.64	1.92	13.72	0
		86 -108	C_1	5.3	5.13	34.12	1.16	14.18	31.15	.16	.53	.59	.73	.57	.21	16.36	4.59	11.77	0
		180 -198	C_3	6.5	4.95	39.29	.46	7.34	32.08	.28	.20	1.46	1.02	.40	.35	17.41	5.00	12.41	0
4	Porters loam, North Carolina	0 - 4	A	11.0	4.68	29.58	.84	8.45	28.62	.04	.36	1.02	1.06	.62	.47	29.13	16.41	12.72	0
		14 - 48	B_2	36.6	5.05	36.33	.64	8.03	36.39	.03	.20	.58	.74	.36	.20	16.75	2.18	14.57	0
		72 - 96	C_2	5.2	5.10	39.74	.22	2.13	38.41	.12	.24	.30	.52	.38	.24	18.32	3.91	14.41	0
5	Durham sandy loam, Georgia	0 - 7	A	2.9	5.52	36.48	.40	5.58	33.33	.07	.52	.86	1.39	.44	.30	21.34	7.97	13.37	0
		51 - 73	C_1	15.7	4.67	38.06	.40	4.11	39.14	.03	.46	.64	1.06	.30	.19	16.37	2.36	14.01	0
		91 -102	C_3	1.7	5.10	25.92	.26	2.45	43.26	.03	.52	.70	.93	.38	.43	25.66	6.83	18.83	0
		103 -110	C_4	2.8	5.47	22.41	[b]	2.33	41.68	[b]	.40	.50	1.18	.60	1.28	29.56	11.26	18.30	0
6	Houston clay, Alabama	0 - 4	A	52.1	4.90	44.60	.57	8.68	25.69	.02	1.61	1.78	1.14	.67	.25	15.07	5.66	9.41	0
		5 - 36	B	65.1	4.73	45.39	.58	9.02	27.03	.03	1.47	1.62	.97	.68	.21	13.71	3.95	9.76	0
		37 - 68	C	64.7	5.60	47.10	.70	8.72	25.84	.02	1.83	1.86	1.01	.50	.37	12.87	3.22	9.65	0
[a] 7	Barnes silt loam, South Dakota	0 - 2½	A_0	22.8	6.40	40.98	.50	9.08	15.35	.25	1.76	2.22	1.83	.09	.41	28.64	17.76	10.88	0
		14 - 48	B_2	20.15	7.22	46.84	.56	11.74	18.35	.17	1.40	3.02	1.36	.11	.29	16.83	7.77	9.06	0
		60 - 78	C_2	11.31	8.45	51.74	.54	11.74	17.36	.13	1.70	3.80	1.98	.15	.18	10.32	2.33	7.99	1.27

[a] Determinations of MnO, K_2O, Na_2O, P_2O_5, and CO_2 as carbonates in colloid samples from profiles Nos. 1 and 7 by G. Edgington.
[b] Trace.

The analytical data given in Table 3 show that in certain profiles the colloids are fairly constant in composition in all horizons but that in other profiles they vary rather widely. For instance, the colloids in the Houston profile (No. 6) are essentially similar in composition throughout the profile. In the Durham profile (No. 5), however, marked variations are to be noted in silica, alumina, phosphoric acid, and in combined water. In nearly all profiles the iron content varies considerably, the highest concentration occurring usually in the A and B horizons. The percentage of the bases shows little variation with depth except in the colloid from those profiles which have developed from glacial material, Nos. 1 and 7. In the colloid from all other profiles the bases are relatively low at all depths. Organic matter instead of being very low in the colloid of the lower horizons, as might be expected, is actually present in considerable quantity in the colloids from the C horizons. The quantities of colloid, however, are very small in the deepest parts of the profile, and small amounts of organic matter penetrating to these depths make up a large proportion of the total colloid. This concentration of organic matter in certain horizons tends to obscure the extent of variation or constancy of the colloid and also the magnitudes of the major constituents. These effects are avoided by recalculating the results to the inorganic basis. The effect of CO_2 as carbonates is also eliminated. The data are given in Table 4.

TABLE 4.—*Major constituents of soil colloidal materials, the results being expressed as percentages of the inorganic material minus CO_2 as carbonates*

Profile No.	Soil	Depth in inches	Horizon	SiO_2	Fe_2O_3	Al_2O_3	Combined water	Molecular ratio $\frac{SiO_2}{Al_2O_3+Fe_2O}$
1	Emmet	1 - 4	A_1	48.48	7.59	23.19	12.46	2.94
		24 - 33	B_1	43.91	13.74	21.70	11.36	2.45
		48 - 60	C_2	47.66	13.40	15.18	6.80	3.40
2	Cecil	0 - 5	A	35.55	12.12	33.22	15.47	1.47
		5 - 36	B_1	33.28	14.09	35.61	14.15	1.27
		72 - 96	C_1	29.30	10.42	39.70	16.67	1.08
		112+	C_3	29.31	4.88	41.37	16.08	1.11
3	do	½ - 4	A	33.41	12.45	35.91	12.59	1.30
		17 - 22	B	30.48	14.33	37.32	13.99	1.11
		86 -108	C_1	35.76	14.86	32.65	12.33	1.44
		180 -198	C_3	41.36	7.73	33.27	13.06	1.82
4	Porters	0 - 4	A	35.38	10.11	34.23	15.21	1.48
		14 - 48	B_2	37.14	8.21	37.20	14.89	1.49
		72 - 96	C_2	41.35	2.22	39.97	15.00	1.70
5	Durham	0 - 7	A	39.64	6.06	36.21	14.42	1.68
		51 - 73	C_1	38.98	4.21	40.09	14.38	1.55
		91 -102	C_3	27.82	2.63	46.43	20.21	.99
		103 -110	C_4	25.25	2.62	46.97	20.62	.88
6	Houston	0 - 4	A	47.28	9.20	27.23	9.97	2.43
		5 - 36	B	47.25	9.39	28.14	10.16	2.35
		37 - 68	C	48.66	9.01	26.70	9.97	2.55
7	Barnes	0 - 2½	A_3	40.96	11.04	18.18	13.23	3.30
		14 - 48	B_2	50.78	12.73	19.90	9.82	3.09
		60 - 78	C_2	57.02	12.94	19.13	8.80	3.55

Both silica and alumina vary in a regular manner in all profiles in which the colloid is not practically constant in composition. This variation, however, is not always in the same direction. In the Durham profile the percentage of silica decreases markedly with depth, whereas alumina increases. In the Porters profile, however, both silica and alumina increase from the surface downward.

The variation of silica in relation to the combined values for alumina and iron is shown by comparing the silica-sesquioxide ratios of the colloids in the various horizons. In the case of three profiles, Nos. 1, 3, and 4, the ratio decreases from the parent material toward the surface, following the order which might reasonably have been predicted. The older colloid in the surface horizons having been subjected to extensive leaching would be expected to have lost silica, thereby narrowing the ratio. In two other profiles, Nos. 2 and 5, the silica-sesquioxide ratio follows the reverse order, being smallest in the colloid isolated from the parent material and increasing regularly toward the surface. The lowest ratios are associated with unusually high values for combined water, namely, about 20 per cent.

FRACTIONATION OF THE COLLOIDAL MATERIAL

The unusually high percentages of alumina and combined water and the low percentages of silica in the colloid samples from the C_1 and C_3 horizons of profile No. 2 and from the C_3 and C_4 horizons of profile No. 5 (Table 4) indicated the presence in these colloidal materials of free hydrated alumina. These samples were obtained from horizons of decomposing rock whose compositions (Table 2) indicated extensive mineral alteration although relatively slight amounts of colloid were isolated. It would seem to follow that the bulk of the colloid present in these horizons forms a part of the partially altered mineral particles, the colloid existing presumably on the surfaces. This colloidal material, it was thought, might consist of hydrated alumina from which the siliceous colloid in the form of aggregates might be separated by some mechanical means.

Previous attempts by Robinson and Holmes (*9*) to fractionate soil colloidal material gave negative results. They concluded that separate colloidal particles differing in composition probably did not exist in the colloidal mixture. This conclusion, however, was reached from a study of colloids from the A and B horizons only and may not hold for colloid in the lower parts of the C horizon, where the colloid is perhaps not so intimately mixed.

The soil samples selected for fractionation of colloidal material were those whose colloids gave indications of containing free alumina. These samples were from the C_1 and C_3 horizons of profile No. 2 and from the C_3 and C_4 horizons of profile No 5. (Table 4.) In addition to these samples two others were selected, the C_1 horizon of profile No. 5 and the C_3 horizon of profile No. 3. Two colloid fractions from each of the six samples were prepared. The first fraction was made as follows: A 10 to 20 gm. sample of soil material was moistened with water and the mass worked to a somewhat plastic consistency by rubbing the particles between the fingers. A small quantity of water made alkaline with ammonia was then added and after settling for a few minutes the suspension was decanted into a 500 c. c. glass cylinder. The settled portion was rubbed between the fingers as before, and the process continued until the cylinder was filled. The suspension was now allowed to settle until microscopic examination showed that the suspension to a certain depth was practically free of particles more than 1 micron in diameter. The colloidal solution was then drawn off to this depth and evaporated to dryness. The second fraction was prepared in a similar manner except that the silty mate-

rial obtained by removal of the greater part of the colloid (explained under Methods) was employed instead of the soil material. In preparing this second fraction about 50 gms. of material were dispersed in 3 liters of water (alkaline to phenolpthalein) contained in a beaker and the colloidal solution drawn off when nearly all particles more than 1 micron in diameter had settled. The quantities of colloid obtained in all cases were very small, averaging not more than 0.5 gm. This was in consequence of the fact that the soil material of the C horizons contained very little colloid and of the fact that this colloid in the case of the silty materials had previously been largely removed. This scarcity of material necessitated the use of samples for analysis much smaller than those customarily taken, with the result that determinations of the constituents present in small amounts were affected by unusually large errors of analysis. The values given for the mono and divalent bases in Table 5 are, therefore, to be considered as only approximate and may in certain cases depart widely from the true values.

In Table 5 are shown: (1) The composition of fractions of colloidal material obtained by an incomplete dispersion of soil material in water, and (2) the composition of colloidal material obtained by dispersing the corresponding silt fractions from which the greater part of the colloid had previously been removed. The composition of these colloid fractions is compared in the table with the composition of the gross colloidal materials previously given in Tables 3 and 4. This material was obtained by alternate dispersion of the soil material and centrifuging of the suspension until nearly all the colloidal material was removed. There are available then for comparison with this gross colloid the composition of fractions differing in thoroughness with which the soil material was dispersed.

It will be seen from Table 5 that in the case of the horizons below the C_2 horizon the two colloid fractions differ materially in composition from the gross colloidal material. The fractions with a few exceptions contain less silica and more combined water than the corresponding gross colloids. The values for combined water in the case of two fractions are especially noteworthy, being 35.33 and 37.39 per cent. Alumina is seen to be highly variable. It is usually present in greatest amount in the colloid fraction from the soil material and least in the colloid fraction from the silt material. The composition of the bases is generally irregular and shows rather wide variations in the colloids from the same horizon and from different horizons of the same profile. The percentages of calcium oxide, however, seem to follow a rather definite order, being greatest in the colloid from the silt material, less in the colloid fraction from the soil material, and least in the gross colloidal material. The lowest values for magnesia appear usually in the colloid fraction from the soil material. Marked irregularities are shown by the alkalies, but the values given may not in all cases be significant. Phosphoric acid is in most cases extremely high in the colloid fraction from the silt material. It is present in least amount in the gross colloid. The extraordinarily high values for phosphoric acid shown by the two colloid fractions from the C_3 horizon of profile No. 2, 12 and 19 per cent, would indicate the presence of some phosphate of aluminum in these colloids. Organic matter is invariably highest in the colloid fractions from the silt material and least in the fractions from the soil material. These facts indicate that in these soils the difficultly dispersible colloid is largely organic in nature.

TABLE 5.—*Percentage composition of soil colloidal fractions compared with compositions of gross colloidal materials*

Profile No.	Soil	Depth in inches	Horizon	Nature of material	SiO_2	TiO_2	Fe_2O_3	Al_2O_3	MnO	CaO	MgO	K_2O	Na_2O	P_2O_5	Ignition	Organic matter	Combined water
5	Durham	51–73	C_1	Colloid fraction from silt material	29.44	(a)	4.27	30.00	(b)	1.70	0.50	2.09	1.94	1.82	29.09	(b)	(b)
				Colloid fraction from soil material	38.19	0.35	5.48	36.94	(b)	.42	.55	.76	.29	.37	15.40	1.57	13.83
				Gross colloidal material	38.06	.40	4.11	39.14	0.03	.46	.64	1.06	.30	.19	16.37	2.36	14.01
		91–102	C_3	Colloid fraction from silt material	13.35	0	3.31	37.85	(b)	3.51	.80	2.34	1.17	2.61	35.84	12.45	23.39
				Colloid fraction from soil material	16.91	0	3.03	49.45	(b)	.92	.37	1.52	2.17	1.38	26.20	1.34	24.86
				Gross colloid material	25.92	.26	2.45	43.26	.03	.52	.70	.93	.38	.43	25.66	6.83	18.83
		103–110	C_4	Colloid fraction from silt material	11.50	(a)	3.65	27.32	(b)	.61	.77	.75	.98	3.32	50.76	13.37	37.39
				Colloid fraction from soil material	20.90	(a)	2.15	45.04	(b)	.42	.38	(b)	(b)	1.47	27.47	3.27	24.20
				Gross colloidal material	22.41	(a)	2.33	41.68	(a)	.40	.50	1.18	.60	1.28	29.56	11.26	18.30
2	Cecil	72–96	C_1	Colloid fraction from silt material [c]	27.54	1.04	7.60	32.06	(b)	1.00	1.98	.28	1.76	1.86	23.70	8.93	14.77
				Colloid fraction from soil material	28.68	1.08	10.95	39.84	.14	.23	.14	.18	.09	.78	17.37	.86	16.51
				Gross colloidal material	28.20	1.12	10.03	38.21	.15	.24	.70	.74	.32	.84	19.82	3.76	16.06
		112+	C_3	Colloidal fraction from silt material	11.08	0	2.60	30.94	(b)	1.24	.62	1.07	0	19.11	33.22	8.60	24.62
				Colloid fraction from soil material	19.97	(a)	1.99	37.88	(b)	.60	.42	.60	.55	11.89	24.32	2.51	21.81
				Gross colloidal material	26.42	.46	4.40	37.30	.08	.42	1.33	1.43	.24	3.44	24.30	9.85	14.50
3	do	180–198	C_3	Colloid fraction from silt material	25.43	.31	4.05	21.22	(b)	1.18	1.45	(b)	(b)	.65	42.74	7.41	35.33
				Colloid fraction from soil material	33.79	.57	8.26	28.04	(b)	.45	.99	(b)	(b)	.76	24.58	2.79	21.79
				Gross colloidal material	39.29	.46	7.34	32.08	.28	.20	1.46	1.02	.40	.35	17.41	5.00	12.41

[a] Trace. [b] Not determined. [c] Analysis by G. Edington.

In order to make a more careful study of the proportions of the major constituents the values for these constituents shown in Table 5 were corrected for the organic matter in the samples. These values are shown in Table 6.

TABLE 6.—*Major constituents (percentage) of soil colloid fractions and of gross colloidal material*

[Results on inorganic basis]

Profile No.	Soil	Depth in inches	Horizon	Nature of material	SiO_2	Fe_2O_3	Al_2O_3	P_2O_5	Combined water	Molecular ratio $\frac{SiO_2}{Al_2O_3+Fe_2O_3}$
				Colloid fraction from silt material.	(a)	(a)	(a)	(a)	(a)	1.50
		51- 73	C	Colloid fraction from soil material.	38.80	5.56	37.53	0.37	14.05	1.60
				Gross colloidal material.	38.98	4.21	40.19	.19	14.35	1.55
				Colloid fraction from silt material.	15.24	3.78	43.23	2.98	26.71	.57
5	Durham	91-102	C	Colloid fraction from soil material.	17.04	3.07	46.43	1.40	25.20	.56
				Gross colloidal material.	27.82	2.63	50.12	.46	20.21	.99
				Colloid fraction from silt material.	13.16	4.21	31.53	3.83	43.16	.66
		103-110	C_4	Colloid fraction from soil material.	21.61	2.22	46.56	1.52	25.02	.77
				Gross colloidal material.	25.25	2.62	46.97	1.44	20.62	.88
				Colloid fraction from silt material.	30.24	8.34	35.21	2.04	16.22	1.08
		72- 96	C_1	Colloid fraction from soil material.	28.95	10.29	39.23	.86	16.52	.97
				Gross colloidal material.	29.30	10.42	39.70	.87	16.67	1.27
2	Cecil			Colloid fraction from silt material.	12.12	2.60	33.85	20.90	26.93	.58
		112+	C_3	Colloid fraction from soil material.	20.48	2.04	38.85	12.20	22.37	.87
				Gross colloidal material.	29.31	4.88	41.37	3.82	16.08	1.11
				Colloid fraction from silt material.	27.46	4.26	22.92	.70	38.16	1.82
3	...do	180-198	C_3	Colloid fraction from soil material.	34.76	8.50	28.84	.78	22.42	1.10
				Gross colloidal material.	41.36	7.73	33.77	.37	13.06	1.82

(a) Not calculated.

The effect of calculating the data of Table 5 to the inorganic basis has been to increase markedly the values of alumina and combined water in those samples in which organic matter was abundant. The values for alumina on the inorganic basis show a regularity not observed in Table 5. The highest values for alumina are found in the gross colloidal material and the least in the fraction from the soil material. It will be observed, however, that low values for alumina are associated with high values for combined water. If the values for alumina in the three colloids of each horizon are calculated to the same water content, the differences in alumina largely disappear.

One of the most significant features of the data of Table 6 is the marked differences in the silica-sesquioxide ratio shown by the groups of three colloids. In the case of the colloids from the C_3 and C_4 horizons of profile No. 5, the ratios of silica to alumina plus iron in the colloid fractions are much lower than the corresponding values in the gross colloidal material. The low ratios observed in the case

of the fractions from the C_3 horizon of profile No. 2 are in consequence of the fact that a considerable part of the alumina present is combined with phosphoric acid and is, therefore, not properly a part of the colloid complex. It is evident, of course, that none of the fractions are composed entirely of material of definite composition, since a sharp separation of definite kinds of colloid was not possible. It may be assumed from the fact that the silica-sesquioxide ratio apparently may diminish to zero that one component of the mixture is free hydrated alumina.

DISCUSSION

The colloidal material of certain of the horizons studied appears to be a mixture of hydrated alumina associated chiefly with the mineral portion of the soil and of siliceous colloid occurring chiefly as colloidal aggregates. Incomplete dispersion of the soil material removed chiefly the aluminous colloid, since the rubbing of the material was insufficient to disperse the siliceous aggregates. In the course of the more thorough dispersion required to remove the bulk of the colloidal material, these aggregates were broken down as is shown by the relatively high percentages of silica in the gross colloidal material. However, after removal of practically all of the colloid present as aggregates, succeeding fractions of colloid were aluminous.

The presence of free alumina in the lower horizons of the soil profile does not mean necessarily that the alumina was produced in those horizons. The downward movement of sesquioxides from the A to the B horizon is, of course, a characteristic feature of podsolic soils. In fact, it has been pointed out that iron may be removed from the soil profile and accumulated elsewhere as bog iron ore. That alumina may penetrate to great depths in the soil profile, however, has not been recognized. The mobility of alumina in the soil depends, of course, on the stability of alumina sols under the conditions prevailing in the soil. Among these conditions may be enumerated the following: Reaction of the soil, concentrations of anions and cations, and the relative concentrations of sols of alumina, silica, iron, and organic matter. Since these factors are closely interrelated it would be very difficult to evaluate them in the case of any one soil. It is interesting, however, to consider these factors in a general way.

Magistad (*6*) concluded that alumina in amounts greater than 3 parts per million can exist in the soil in solution only when the reaction is more acid than pH 4.7 or less acid than pH 8. From pH 5.4 to pH 7 the amount of alumina in solution is usually less than a part per million. However, Joffe (*5*) points out that these values are valid in the presence of the sulphate anion only. In fact, according to Joffe the sol state of alumina can not exist in the presence of the sulphate ion. In the presence of the chloride ion the sol exists from pH 4.3 to pH 5; at the latter value most of the alumina is in the gel state. The nitrate ion influences the state of aggregation in about the same manner as the chloride ion.

In regard to the effect of organic-matter sols on the stability of alumina sols Aarnio's work (*1*) may be cited. Aarnio found that whereas iron oxide sols were stabilized by organic matter if the concentration of organic matter was three times that of the iron oxide, alumina sols required thirty times more humus than alumina to effect

stabilization. He concluded from this relationship that aluminum precipitates under all circumstances since such concentrated humus sols do not usually exist in nature.

The presence of considerable quantities of organic matter in the colloid fractions obtained by dispersing the silt material suggests the possibility that alumina may have penetrated to the lower horizons under the stabilizing effect of soluble organic matter. From Aarnio's work, however, it would seem that conditions favored the accumulation of ferric oxide in these lower horizons rather than alumina. The composition of the colloid fractions, however, gave no indication that ferric oxide had accumulated.

The recent work of Mattson (*7*) on the mutual flocculation of alumina and silica solutions is of interest in considering the possibility that alumina may have penetrated downward under the stabilizing action of silica. Mattson (*7, p. 302*) concluded that "the alumina-silica system forms isoelectric precipitates in which the proportion of silica decreases with an increase in pH, approaching zero at pH 7 at which point the alumina is itself isoelectric." According to Mattson alumina and silica in the molecular ratio of 1 to 1 would be flocculated at pH 6.6, and a mixture of silica to alumina in the ratio of 6 to 1 would flocculate at pH 5. These relationships are sufficient to render the transport of alumina under the protective action of silica highly improbable in the soils under study.

Although no definite conclusion can be reached as to the mobility of alumina in these particular soils, it has been seen that soil conditions are in general unfavorable to the downward movement of alumina below the B horizon. In the absence of evidence that alumina has moved downward in these soils it is important to consider the possibility that the alumina may have been formed in the horizons in which it occurs.

Evidence was offered earlier in this paper which indicated that mineral particles in certain of the horizons were highly altered although relatively little colloid could be isolated from the horizons in question. This condition was accounted for by assuming that the greater part of the colloidal material present in these horizons was contained on the surfaces of certain mineral particles, relatively little being present in the form of aggregates. It has been shown that colloid fractions prepared by further dispersion of silt material from which the greater part of the colloid had previously been removed contained a higher proportion of alumina to silica than was present in the gross colloidal material. It is reasonable to conclude, therefore, that this excess alumina was present on the surfaces of mineral particles rather than as colloidal aggregates. It might be assumed, of course, that the alumina was derived from difficultly dispersible aggregates consisting chiefly of colloidal alumina. This explanation, however, is rendered improbable by the fact that the colloid fractions prepared by partial dispersion of the soil material were similar to those prepared by dispersing the silt fractions, the differences between the two fractions being chiefly in degree of hydration. Furthermore, the large amounts of combined water contained in several of the colloid fractions indicate the relatively recent origin of the material.

The alumina present in the horizons investigated may be regarded as derived from some intermediate alteration product of silicate min-

erals. Kaolinite is perhaps too resistant to alteration to have produced the alumina, but halloysite, its amorphous equivalent, may have been the intermediate alteration product from which the alumina was derived. The association of halloysite with bauxite and the alteration of plagioclase feldspars to bauxite are, perhaps, significant in this connection.

The conclusions reached in regard to the origin of colloidal alumina in these soils are wholly tentative, further inquiry having been terminated by the author's transfer to another bureau. The data are published at this time by reason of their unique nature. Conclusions suggested by the data should be tested by further investigation.

SUMMARY

This investigation deals with the composition of colloidal material in the horizons of the soil profile. Colloidal material was isolated quantitatively from seven soil profiles representing a wide range of composition and profile characteristics. It was found that in some profiles the colloidal materials were fairly constant in composition; in other profiles the colloids varied rather widely. The constituents in which variations were most general were silica, alumina, iron, organic matter, and combined water. Except in the case of profiles developed from glacial material the percentages of the bases showed little variation with depth and were low in all horizons. Silica and alumina varied regularly in all profiles in which the colloids were not practically constant in composition. These variations, however, were not always in the same direction.

The molecular ratio of silica to alumina plus iron showed in the case of colloids from several profiles a regular decrease with depth, indicating that extent of weathering was not the chief factor tending to reduce this ratio. The relatively low silica-sesquioxide ratios were attributed to the presence of free hydrated alumina in the colloidal material of the lower horizons. Further evidence of the presence of free alumina was obtained by fractionating the colloid showing a low silica-sesquioxide ratio. The colloidal fractions were found to contain a higher proportion of alumina to silica and more combined water than the gross colloidal materials. The presence of free alumina in the colloid of the lower horizons was accounted for on the assumption that colloidal material existing on the surfaces of altering mineral particles contains free alumina.

The relatively high percentages of alumina and combined water in disintegrated but apparently undecomposed parent rock and the low pH values of this material indicate that some of the minerals composing this material have undergone extensive alteration.

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